A CENTURY OF PROGRESS IN THE NATURAL SCIENCES

A CENTURY OF PROGRESS IN THE NATURAL SCIENCES

1853-1953

PUBLISHED IN CELEBRATION OF
THE CENTENNIAL OF
THE CALIFORNIA ACADEMY OF SCIENCES

California Academy of Sciences
SAN FRANCISCO
1955

Dedicated to the memory of

JOHN WARD MAILLIARD, JR.

in appreciation of his long and faithful service as a Trustee and as Chairman of the Board, of his many benefactions to the Academy, and of his stimulating faith in its future

FOREWORD

This volume of essays has been prepared as part of the recognition of the Centennial of the California Academy of Sciences. In May, 1951, three members of the Council were authorized by the Trustees of the Academy to make plans for a volume of scientific papers appropriate to the occasion. After careful consideration the committee decided that a most appropriate central theme for the volume would be the historical treatment of biosystematics, using this term in the literal sense, namely, the systematic treatment of living things and with emphasis on developments since the founding of the Academy a century ago.

This theme appealed to the committee as especially appropriate since it was during this period, from the middle of the nineteenth to the middle of the twentieth century, that the basic principles underlying our present concepts and aims in the classification and systematic treatment of organisms were clearly enunciated and definitely accepted among biologists. The nineteenth century brought to biology two all-important contributions, Darwin's and Wallace's conception of organic evolution and Mendel's principles of heredity. Recognition of the doctrine of organic evolution led directly to the working concepts of the continuity of species and the transformation of old species into new ones. Recognition of the basic laws of heredity has led, in the twentieth century, to very great progress in the development of our concepts of the nature of the evolutionary processes.

It was inevitable that these tremendous forward steps should have a profound impact on the thinking and practices of those systematists who recognize the significance of the facts, not only of comparative morphology, but also of variation and heredity and of the contributory disciplines of cytogenetics, physiology, biochemistry, serology, biometry, ecology, and biogeography. Inevitable too was the apathy shown toward these epoch-making advances by many taxonomists who were content to pile up new names of species and genera without critical study of all available criteria of relationship, thus creating a maze of names rather than systematics. Although some taxonomists are still littering the waysides of biological literature with unnecessary names, there is a growing tendency among systematists to bring to bear upon problems of classification and nomenclature all of the various categories of evidence that are available in order that the decisions reached shall represent as nearly as possible the true state of nature. This modern viewpoint and aim is the culmination of many experiments in the systematic treatment of organisms prior to and extending throughout this "Darwinian" century.

It is only in recent decades, however, that the advantages of the many-sided attack on problems of relationship and phylogeny have been realized. Many obscure problems in the relationship of organisms have been cleared up by the evidence from cytology, genetics, and biochemistry, not to mention other contributory disciplines; and, in many instances, such evidence has resulted in radical changes in older taxonomic treatments. At the same time, it has been clearly demonstrated that the evidence on relationship provided by the "newer" disciplines corroborates in the main the earlier systematic treatments that were devised by taxonomists who based their schemes primarily on comparative morphology. Certainly due credit should be given to the many "specimen taxonomists" who have labored through the centuries, often without fair recognition from other biologists and under great difficulties, in their conscientious efforts to bring hitherto unknown organisms into some sort of classificatory system. Without their invaluable services the general advance of biology would not have been possible.

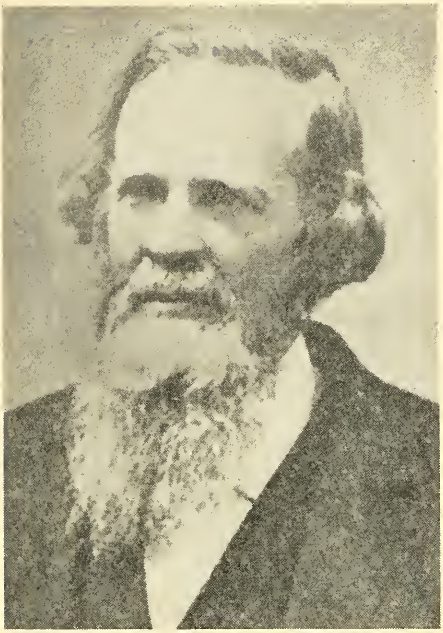
Most of the essays in this volume attempt to review the progress made during the past century in the classification of organisms. The original plan of the volume included all the major groups of organisms. It was found impossible to achieve this degree of completeness; but except for a few gaps the earth's organic life is well represented and the committee consider it a great honor to be able to present to the biological world this series of authoritative historical reviews.

In the exploratory phase of plant and animal classification the services of field workers, especially of trained naturalists, are indispensable. Much of the activity of the California Academy of Sciences has been concerned with the collection and preservation of specimens. It seemed appropriate, therefore, that the first essay should deal with naturalists and the early days of the Academy. The following chapter presents a review of the beginnings of geodesy and astronomy in California because this Academy was so closely tied in with those events; and the third essay is a stimulating contribution by a philosophically minded biosystematist. Then follows the series of systematic reviews, together with four essays which do not treat of major groups of organisms—one on invertebrate paleontology, two on biogeography, and one on wildlife conservation. In all of these essays the disciplines represented are largely, but with some additions, those which have come within the purview of the California Academy of Sciences.

The committee are confident that this volume will long serve as a most valuable source book in the history of science.

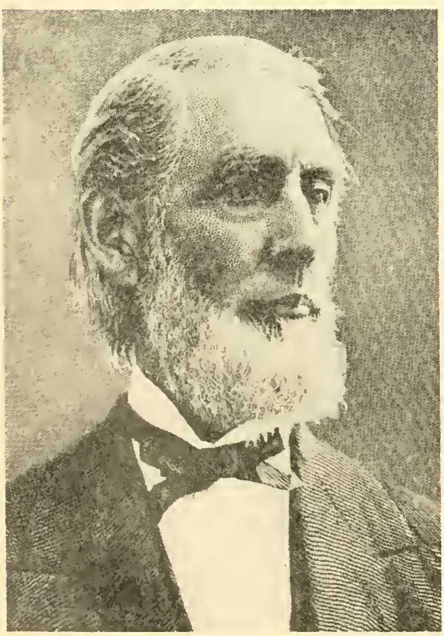
ERNEST B. BABCOCK
J. WYATT DURHAM
GEORGE S. MYERS

CONTENTS



ALBERT KELLOGG

JOHN B. TRASK



HENRY GIBBONS

THOMAS J. NEVINS

SAN FRANCISCO AS A MECCA FOR NINETEENTH CENTURY NATURALISTS

With a Roster of Biographical References to Visitors and Residents

By JOSEPH EWAN
Tulane University

As THE GENUS is first identified by the distinctness of its species, so the country is first distinguished by its most prominent city. Charleston served as the germ of Carolina, New Orleans of Louisiana, Lima of Peru, Montevideo of Uruguay, and San Francisco of California. California, a vast and diversified country, was an island on the edge of El Dorado, said to be fabulous and fortunate, sought by many, reached only with difficulty, and San Francisco was her heart. Even before the Gold Rush, to come to California from European cities amounted to a journey half way 'round the world. And for the American back in the "States" coming to the City of the Golden Fifties was not just going across the Shenandoah to a frontier valley, or just setting out west from Albany, or even the equivalent of taking a clipper ship out of a New England port or New York for Charleston or Apalachicola or New Orleans, but a voyage to a land far away, hemmed in by the Humboldt Sink and the Sierra Nevada, and peopled by men and women who had a different derivation and who spoke a different language. Very early in the history of California reports came back of giants and riches, where ordinary things were extraordinary, and superlatives were elementary parts of speech. Great flocks of wildfowl in the marshes, grizzly bears that challenged the bravest men, giant birds (the California condor), giant trees, and giant seaweeds. Even the slugs in settlers' gardens were enormous! But it was those giant nuggets of gold! The spirit of the Seven Cities of Cibola lives on.

Naturalists have always been in the vanguard of explorers: so it was in California. With a party of prospectors who took the Gila Trail came Audubon's son, John Woodhouse Audubon,[1] and with a party of trappers following the trail west from Santa Fe, came William Gambel. Most of these naturalist adventurers in the Great West were young men between the ages of nineteen and thirty years. Some were serious naturalists trained in the essentials of the natural sciences, either with field experience or with training in medicine, apprentices to an apothecary or a taxidermist's helper. A few, like John Woodhouse Audubon, Isaac J. Wistar, Titian Ramsey Peale, and John Lawrence LeConte, were scions from old naturalist rootstocks. Some of these emigrant naturalists would cast their lot to stay in California—and California meant in the cultural sense San

1. For biographical notices of naturalists mentioned in this account see the appended roster.

Francisco—to share in the founding and the support of the California Academy of Sciences.

Naturalists in San Francisco Before 1853

In 1939 Alice Eastwood summarized the history of botanical exploration on the Pacific Coast and four years later Roland H. Alden and John D. Ifft published in the Occasional Papers of the Academy a review entitled "Early Naturalists in the Far West." For this reason the notice given here to naturalists active before 1853 will be brief.

The first naturalists to visit San Francisco were French explorers under Comte de La Pérouse who made a landfall there in 1786. La Pérouse was commander of the *Boussole,* and with him was the gardener and botanist, Jean Nicholas Collignon, while the corps of the second vessel, *Astrolabe,* included De Boissieu la Martinière, "doctor of physic and botanist," and the naturalist, Louis Dufresne. Six years later, in November, 1792, Captain George Vancouver visited both San Francisco and Monterey and Archibald Menzies, surgeon-naturalist to the expedition, took back to England the California condor (perhaps taken along the lower Columbia River) but was able to collect only a few plants. In 1806 another flag entered San Francisco Bay, representing a nation that had as yet not challenged the Spanish supremacy in California. On March 28, 1806, the Russian ship *Juno* sought supplies for Russia's stricken colony at Sitka, the base of her fur seal operations in the North Pacific. Langsdorff, an officer on board the *Juno,* has left us a detailed account of the forty-four days at anchor here.

The Russian settlement was established at Fort Ross in 1812, primarily to supply fresh vegetables for the scurvy-cursed men plying the boats in the Behring Sea for seals. Trading vessels were not allowed to enter any port of California at this time and Russians from Fort Ross who ventured into San Francisco were held prisoners there by the Spanish for violations of the laws. It is unlikely, therefore, that the Russians were able to collect many specimens in the region at this time.

Ten years passed before a second Russian vessel, the *Rurik,* carrying another surgeon-naturalist, Johann Friederich Eschscholtz, entered San Francisco harbor on October 1, 1816. Captain Kotzebue carried with him on the *Rurik* the well known poet and naturalist Adelbert von Chamisso. Though the visit of the *Rurik* was made during the late fall dry season the expedition collected a large number of novelties because of unusual rains.

Kotzebue visited San Francisco for the second time in 1824 and Dr. Eschscholtz again accompanied Kotzebue. The Russian ship spent nearly two months in California, leaving San Francisco on November 25, 1824. The captain opined: "I confess I could not help speculating upon the benefit this country would derive from becoming a province of our powerful empire, and how useful it would prove to Russia." Eschscholtz's collections were exclusively zoological on this second voyage. He died in 1831 before the completion of his *Zoologischer Atlas,* in which he published his Californian discoveries.

During the last years of the Russian occupation several Russian naturalists visited northern California. These included Governor Ferdinand P. Wrangell; Dr. F. Fischer and Dr. Edward L. Blaschke, of the Russian American Company;

the agriculturist, George Tschernikh, and I. G. Vosnesensky, curator of the Zoological Museum of St. Petersburg. The plant collections of Vosnesensky came back to San Francisco, to the Academy, after lying in their herbarium covers for nearly a hundred years in Russia. The collections were returned to California for identification by John Thomas Howell, and then sent to Leningrad's national herbarium.

In 1824 hide ships began operating along the California coast. These vessels were the source of introduction of many organisms, some injurious: insects, weeds, and rodents. This traffic in hides marked the reintroduction of some weeds earlier introduced with the Mission Period which began in 1769 with the founding of Mission San Diego. One of these ships took on a little piece of immortality, for it was the *Alert* that carried Thomas Nuttall from California around the Horn, with that commentator of the day, Richard Henry Dana.

The British expedition under Captain Beechey visited California in 1827. The natural history collections were made on the voyage of H.M.S. *Blossom* by the ship's surgeon, Dr. Alexander Collie, assisted by George Tradescant Lay, and Lieutenant Belcher. The *Blossom* was in port twice, from November 7 to December 28, 1826, and November 19 to December 3, 1827. Dr. Collie collected the type specimens of thirteen species of birds either at San Francisco or Monterey, both ports having been visited twice on the voyage.

The French sailing vessel *Héros* put in at San Francisco on January 26, 1827, with a surgeon on board, Dr. Paolo Emilio Botta, who was then twenty-one years of age. Botta collected both birds—including the roadrunner—and plants. The *Héros* spent nearly two years intermittently on the coast, from Fort Ross to San Diego, finally departing on July 27, 1828. The California buckeye, named *Calothyrsus californica* by Spach, was one of Botta's collections.

David Douglas, "Douglas of the Fir," arrived in San Francisco in 1831, following his first highly successful visit to America. His California visit introduced dozens of species to horticulture and to systematic botany. Douglas botanized as far south as Santa Barbara, making the Franciscan missions his lodging places along the route. It is unfortunate that his fieldbooks were lost for few explorers in California natural history would have had so much to tell. "Douglas, no mere collector, was a skilled natural scientist in his own right. Of his character and personality, what more need we say than that he courageously faced adversity for the science he loved, and died in pursuit of knowledge?"

The Irish naturalist, Dr. Thomas Coulter, first served as a physician to a mining company in Mexico before coming to Monterey in 1831, where he met David Douglas in November. Coulter spent nearly three years on the Coast, including a trip to the Colorado Desert, but did not remain on the Coast to meet Nuttall, who closely followed him. Coulter may have met Ferdinand Deppe, a professional collector from Berlin, at Monterey but we have only fragmentary knowledge of Deppe, save that he arrived in California during the winter of 1831–1832, possibly from the Mexican port of Loreto. David Douglas had met Deppe in California sometime prior to October 24, 1832, and Deppe was at Monterey as late as December, 1834, when he shipped bird skins to Lichtenstein, then director of the Zoological Museum of Berlin. The beautiful endemic Matilija poppy, *Romneya coulteri*, was one of Coulter's discoveries in southern California.

Thomas Nuttall and John Kirk Townsend crossed the continent together with

Captain Nathaniel Wyeth, setting out from Independence, Missouri, on April 28, 1834, as members of an original party of seventy men with 250 horses. The Townsend narrative, a model of forthright reporting and a treasure for the serious student of the American West, makes some mention of the events of a botanical and ornithological nature along the way, and gives us concrete evidence of the devotion of Nuttall to science. Finally Nuttall returned 'round the Horn in 1836 but Townsend remained another year on the Coast. Both of their collections ultimately reached Philadelphia, Nuttall dividing his plant specimens between the Philadelphia Academy and his personal herbarium, which ultimately came to rest at the British Museum (Natural History). Audubon purchased Townsend's bird skins and enriched his own ornithological writings thereby. Nuttall "raised himself from a penniless orphan to a highly respected man of science," joining the era of B. S. Barton, his one-time patron, with that of Asa Gray and Elias Durand. Nuttall's travels in America have been delineated by Pennell with documentation, and his California visit has been fraternally told by Jepson.

The London Horticultural Society, which first sponsored David Douglas in America, sent twenty-four-year-old Karl Theodore Hartweg, of Karlsruhe, to Mexico in 1836, and to California in 1846. He arrived in Monterey on June 7 and proceeded north to San Francisco and Chico late that year. His plant collections in the northern Sierra Nevada were particularly valuable. Hartweg's botanical collections fared better than most in that the British systematist George Bentham handled them and published a commentary upon them entitled *Plantae Hartwegianae.* Hartweg's companion on his visit to Bear Valley in the Sierra Nevada was Theodor Cordua, "pioneer of New Mecklenburg," whose account of the trip has recently been translated.

The French frigate *La Vénus,* under command of Admiral Abel du Petit-Thouars, arrived at Monterey, October 18, 1837, and departed November 14. Both zoological and botanical collections were made then and a description of the California visit appears in Thouars' *Voyage autour du monde sur la frigate "La Vénus"* (Paris, 1840–1843, 2: 77–142). The surgeon on the *La Vénus* was Adolphe Simon Neboux, who most likely made the natural history collections. A dexterous piece of detective work involving this French expedition is John Thomas Howell's story "Sea-gulls and Tarweeds: a Distributional Mix-up" *(Leafl. West. Bot.,* 1: 189–191, 1935.).

Richard Brinsley Hinds, surgeon on H.M.S. *Sulphur,* visited the California coast in 1836 and 1839. Hinds was assisted by Barclay and Dr. Sinclair. Their collections on the coast of Baja California were particularly important. Captain Edward Belcher's narrative (London, 1843) contains Hind's report on the "Regions of vegetation . . . of the globe in connexion with climate and physical agents," a rather commonly overlooked essay of considerable interest for the plant geographer.

The six ships that set sail as the United States Exploring Expedition—our first Government expedition—under Captain Charles Wilkes on August 18, 1838, carried six scientists. (There had not been such a concentration since the "Boatload of Knowledge" set off down the Ohio for New Harmony!) The six scientists with Wilkes' Expedition were: Pickering, Brackenridge, Couthouy, J. D. Dana, Titian Peale, and William Rich. The expedition was surveying the Pacific Coast between April 6 and November 1, 1841, and the results were eventually published after prolonged disaffection between Captain Wilkes on one side and the staff and authors who prepared the texts of the various departments of science on the other. That the publication of the results depended on Congressional approval was no small discouragement. Titian Peale reported on the vertebrate collections and Torrey and Gray on the plants, with Pickering publishing a remarkable omnibus volume entitled a *Chronological History of Plants: Man's Record of His Own Existence Illustrated Through Their Names, Uses, and Companionship,* based in some considerable part on his travels with the Wilkes' Expedition.

Captain John Charles Frémont, the "Pathmarker," entered California in 1844 on his first overland expedition. In his diaries he noted trees and items of natural history—he had been instructed by Dr. John Torrey to take dried plants along the route—but in the end he did not bring back many specimens, partly owing to the misfortune of having hard rains ruin his collection. On his expedition of 1846 Frémont paid closer attention to collecting and these specimens were the subject of a memoir by John Torrey.

Keenly aware of the attractions of California as a potential colony for the Crown, H.M.S. *Herald* arrived in Monterey during these days of contested Spanish rule. But the American chronicler Stillman sums up that story in a sentence: "Monterey had already fallen into the hands of the Americans, and she sailed away disgusted." Berthold Seemann, who was later to distinguish himself in the botany of Fiji and other tropic lands, accompanied the *Herald*.

Historian John Walton Caughey says, "Take away the initial bonanza of gold and how much less rapid and how different would the state's rise have been." James Wilson Marshall's discovery of gold on the American River in 1847 set off "one of the most articulate migrations in history," drawing shiploads of emigrants from virtually every country of the world. During the year 1849 several visitors with some interest in natural history arrived in California, some of them members of emigrant parties lured by the activity in the goldfields.

On April 5, 1849, William Gambel, a protégé of Nuttall, who had made the overland trip to California in 1841 via the Gila Route and had returned to Philadelphia with 176 species of birds, joined a party of adventurers bound for the goldfields. The original party divided and Gambel joined those who followed Hudspeth's trail but they were caught by snow in the mountains and only Gambel and a few others reached Rose's Bar on the Feather River. Gambel, sick and exhausted, died of typhoid fever on December 13, 1849. Joseph Grinnell remarked to this writer that Gambel's bird skins—the ones taken on the earlier trip of 1841, the collection of 1849 being lost—were among the best skins he had ever handled. The ornithologist Cassin described Gambel's skins many years ago as "some of the most magnificent specimens I ever saw." Witmer Stone says that Gambel "in the short space of eight years demonstrated that he was possessed of remarkable ability both as an explorer and field naturalist and as a student of natural history."

The New York taxidermist, John Graham Bell, who accompanied Audubon up the Missouri in 1843, reached California in 1849 via the Central American isthmian route. He visited Sutter's Mill and localities from Sonoma to San Diego; considering the short duration of Bell's visit he made a notable collection, taking the types of four birds described as new by Cassin. Bell himself described the

Pacific Coast towhee. It is interesting to contemplate what might have been the history of California ornithology had Bell decided to stay in the State rather than return to New York! He died at Sparkhill, New York, in October, 1889.

John Woodhouse Audubon, son of the famous ornithologist, came overland across Texas and northern Mexico, arriving in San Diego, November 4, 1849. He evidently proceeded to the Sierra diggings directly. The Academy has a direct connection with John Woodhouse Audubon through the late Leslie Simson, mining engineer and sportsman who collected specimens of African big game in Kenya and was also the donor of the California Academy's Simson African Hall. Simson learned taxidermy as a lad from his father, who in turn had been instructed by John W. Audubon.

With Audubon came Dr. John Boardman Trask, cofounder with Dr. David Wooster of California's first medical journal. He was the first resident naturalist to describe the State's recent and fossil shells. His work appeared in Volume One of the Academy's *Proceedings.* Trask, one of the seven founders of the Academy in 1853, later became distinguished as physician, chemist, mineralogist, seismologist, geologist, paleontologist, and botanist.

Particularly versatile was Dr. Jacob Davis Babcock Stillman, perhaps best known for his association with Senator Leland Stanford, whom he served as personal physician. Dr. Stillman was a writer of some merit, and his book entitled *Seeking the Golden Fleece* (San Francisco, 1877) is highly readable for its personal approach. He arrived in San Francisco on August 5, 1849, after 194 days' passage on the ship *Pacific;* the fare from New York was $300. Upon his arrival at Sacramento Stillman began collecting plants, ranging as far afield as Marysville and Long Bar in 1850. Some of this material he sent to John Torrey, and Asa Gray subsequently based *Leptosyne stillmanii* on part of it. Stillman was a classmate friend of Dr. Charles Christopher Parry at Union College, and they worked together occasionally on the smaller problems of the California flora. Stillman refers to "my old college friend, Charley Parry, botanist [of the Mexican Boundary Survey]. Charley is now [1877] on the Gila River." Stillman's friendship for Parry certainly stood Parry in good stead in securing such favors as railroad passes for his collecting trips and the like. Within the pages of the *Overland Monthly,* dear to the heart of the antiquarian, are buried some sparkling paragraphs, and not a few were written by naturalists! One of these stories is "Old Fuller," a vignette of the Day of Resurrection, written by Dr. Stillman.

The Reverend Augustus Fitch was in southern California between 1846 and 1849 and sent a few plants to John Torrey, perhaps through the suggestion of Dr. Parry, but we lack exact knowledge of this fact. There is a note in the Torrey correspondence of the Reverend Fitch finding *Abronia umbellata* at San Francisco and Monterey and pointing out its technical characters.

William Lobb, employee of the large nursery firm of James Veitch, of Exeter, England, arrived in 1849. He had left England at the age of thirty-one and collected seeds and plants in South America before his arrival in California, but his story properly falls a little later in connection with the Big Tree. George Black collected on the Yuba River in 1850; he may have been associated with Lobb but I find no evidence that he was employed by a foreign seed house, and we can only surmise that he may have turned (perhaps unsuccessfully?) from the mines to work with Lobb in the Sierra foothills.

Much less known than Lobb is Dr. Timothy Langdon Andrews, physician and botanical collector, who reached San Francisco in November, 1849, and after a month in the Bay city went to Monterey, the capital of the American colony. There Andrews opened a school and in his leisure time made a large collection of plants in the vicinity. In the summer of 1850 he made a two weeks' horseback trip with William Lobb to the Mission San Antonio de Padua and into the adjacent Santa Lucia Mountains. It is certainly possible that Dr. Andrews met Dr. Parry during his stay at Monterey, but in any event Dr. Andrews made contact with Torrey and Gray, who studied his collections. Gray named the endemic tufted *Galium* of the Coast Ranges for him as a pleasant gesture of one botanist to another. Later Andrews was an inspector of customs in San Francisco and a newspaper journalist, and there he met Dr. Albert Kellogg of the Academy, who must have been delighted with Andrews' wide experiences. Both had lived and traveled in the South before reaching California, Kellogg being a brief resident of Charleston and Andrews of New Orleans.

In the fall of 1850 two great figures in American science arrived in California together: James Graham Cooper, the zoologist, and John Lawrence LeConte, renowned student of beetles and cousin of Professor Joseph LeConte. Dr. Cooper, son of William Cooper of New York, later became prominent in the history of the West as an Army surgeon attached first to the Northern Pacific Railway Survey, then to Mullan's Expedition. Between 1860 and 1862 Cooper was stationed at Fort Mojave, and from there he explored the almost unknown north slope of the San Bernardino Mountains. In 1864 he served with the California Volunteers. After the Civil War came a period as naturalist with the California State Geological Survey. Brewer, whose judgments were generally fair, wrote of him, upon the occasion of his first meeting in 1861 as "a man of more than ordinary intellect and zeal in science, but I fear not a very companionable fellow in camp." Cooper contributed to the text of T. F. Cronise's popular *Natural Wealth of California,* published in 1868. From 1875 until his death in 1902 he lived at Hayward, and his name is commemorated in that of the Cooper Ornithological Club, now "Society." Cooper was interested in mollusks and general zoology, ethnology, and kindred subjects, several of which were the topics of papers contributed to the early volumes of the *American Naturalist.*

In the early days of California's statehood probably every tenth man was a Frenchman. This was owing to two reasons: first, the natural attraction of gold and the untried opportunities in new lands, and, second, the unsettled homeland conditions of France resulting from the revolutionary movements of 1848 on the Continent. One of the Frenchmen who left Paris then was Pierre Joseph Michel Lorquin, pioneer collector of butterflies in California. He said that he came in 1850 for "the number of new things he would be sure to get"! Lorquin traversed much of the State on foot from Plumas County to San Diego, wielding his net and sending the specimens to J. A. Boisduval, who described 83 butterflies and twelve moths from Lorquin's collections. In 1852 Lorquin met Dr. H. H. Behr, who later presented Lorquin's duplicate butterfly types to the Academy, but these were destroyed in the fire of 1906. The Lorquin's admiral, *Basilarchia lorquini* (Boisduval), generally distributed throughout California, is a living memento of this zealous collector of the 'fifties.

The German physician, Frederick Adolphus Wislizenus, came to America in 1835 and is best remembered for his pioneer explorations in Chihuahua. He visited California in 1851, collecting some plants on the American River. Dr. Samuel Washington Woodhouse, surgeon-naturalist with Lieutenant Sitgreave's Zuñi River Expedition of 1851, paused in San Francisco before returning home via Nicaragua. Woodhouse's article on ornithology in Sitgreave's *Report* includes field notes on 219 species of birds. The territory covered is actually greater than the title of the expedition would suggest, since it covered Indian Territory and Texas to California.

The Swedish frigate *Eugénie* paused at San Francisco in 1852 on her voyage around the world. Aboard was the botanist, Nils Johan Andersson, then thirty-one, who later became the most prominent contemporary authority on willows. Dr. Eric Hultén tells me that Andersson's narrative, *En Verldsomsegling* (Stockholm, 1854), which was based closely on his existing diary, contains a description of San Francisco (pp. 98–180), his journey to Sacramento, and the goldfields. But Hultén says Andersson does not record having met any naturalists in California.

The year 1852 saw California's maximum gold production: $81,294,700 that year. San Francisco's part was integral in the State's prosperity and, in the words of Robert Glass Cleland, the historian, "many cities in the United States boast a more ancient lineage than that of San Francisco; but none can look back to a more vigorous, boisterous or interesting youth." From a town of nine hundred souls in the spring of 1848 San Francisco became a bustling market place where "speculation, open-handedness, startling success or equally swift failure, hurry, rush and disregard of caution" were characteristics. A decline in business values set in in 1853, following the boom year in the Mother Lode, but shipping was on the upswing and approximately five hundred vessels were employed in the whaling industry by 1855. Ten years later San Francisco was the headquarters for the whale-oil industry. Significant in the cultural sense was Edwin Booth's playing at the San Francisco Theatre to an appreciative audience.

In the national perspective 1853 saw the beginning of the Pacific Railroad Surveys under Secretary of War Jefferson Davis. For two years these surveys reconnoitered so thoroughly and efficiently that the railroad routes of today were laid out along essentially their original markers. These surveys covered the five transcontinental routes traversed today from the Northern Pacific Railroad to the Southern Pacific Railroad via the Gila Route. Each of the five field parties included a surgeon-naturalist, who collected objects as opportunity afforded. The published reports arising from these surveys served as reference works for the first residents of California, as many well-worn copies of the *Pacific Railway Reports* to be seen in second-hand bookshops today will attest. W. P. Blake was geologist and mineralogist to Williamson's Expedition. "The party will rendezvous at Benicia" were Lieutenant Williamson's instructions. Blake's own papers dealt among other topics with Tertiary Infusoria and "observations on the extent of the gold region." Among other specialists who reported on the results of the expedition were T. A. Conrad on the fossil shells; A. A. Gould on recent shells; Louis Agassiz on fossil fishes; and S. F. Baird on mammals. Four physicians attached to these various surveys, John Milton Bigelow, Thomas Antisell, Adolphus L. Heermann, and John Strong Newberry, all visited San Francisco during this period and must have been welcome wayfarers for Dr.

Kellogg in the city. Dr. Bigelow's collections were the most extensive for central California and more than 1,100 collections were enumerated in Volume Four alone of the *Reports*. Though Dr. Heermann collected in nearly all fields, he was particularly interested in birds and birds' eggs. He introduced, in fact, the word "oology" into ornithological literature. Heermann came to California in 1849, but his activities prior to the Pacific Railway Surveys are unknown. The beautiful Heermann gull places his name in California skies.

What appears to be wholly sound scientific progress was the subject of satire by Lieutenant George Horatio Derby, graduate of West Point in the class of 1846, who wrote a book, *Phoenixiana or Sketches and Burlesques,* under the nom de plume of John Phoenix (New York, 1903). Derby's burlesque on the surveys is entitled "Official Report of Professor John Phoenix, A.M., of a Military Survey and Reconnaissance of the Route from San Francisco to the Mission of Dolores, made with a view to ascertaining the practicability of connecting these points by a railroad." In the same volume appears "The San Francisco Antiquarian Society and California Academy of Arts and Sciences." In this sketch Derby patently parallels the founding of the Academy, beginning with a committee to draw up the constitution consisting of "Dr. Keensarvey, A. Cove, and James Calomel, M.D." Who these characters equate to in real life may test the historic senses!

Founding of the Academy

When the five doctors, a real estate man, and a school superintendent met informally on April 4, 1853, to consider organizing an academy to bring together persons with a collecting urge, or a curiosity to know the singular forms of life that they noticed were different from those "back home," there could have been little notion of the expeditions, comprehensive collections, and reference libraries in the natural sciences that would follow. Though, to speak quite honestly, we know little about some of the men who met that day, they must have had something of the spirit of the Salem merchants who, while they spent most of their time vending staples and making money, always took time to remind their friends, the sea captains, to watch for big conch shells on the next voyage, a nice perfect shell of a Galapagos tortoise, or a better tail feather of the Australian lyre bird than Nicholas Titcomb down the way had just acquired.

Lewis W. Sloat, the real estate man in whose office the "founders" met on old Montgomery Street, was an amateur conchologist and had a cabinet of shells in his office. He does not, however, seem to have been in contact with Eastern naturalists.

Colonel Thomas J. Nevins must certainly have been an idealist, for it was Nevins who, against considerable opposition, persuaded the Common Council of San Francisco to establish a free public school system. This was in 1851. After the first meeting the Academy repaired to Colonel Nevins' office on Clay Street, and they continued to meet there for many years. It was not until 1874 that the Academy moved to larger quarters in Dr. Stone's old brick church at California and Dupont streets. Of two of the five physicians we have little knowledge. Dr. Andrew Randall was selected chairman of the first meeting, and elected president of the Academy three successive years. He was shot by a gambler on July 24, 1856, and the murderer was hanged five days later by the Vigilance

Committee. But what may have been Dr. Randall's natural history interest I do not know. Nor do I know the interests of Dr. Charles Farris, who attended the first and third meetings of the Academy but left the state in the summer of 1853 and was lost track of. The other three physicians were well known citizens of the city and left distinguished records. The youngest of the three when the Academy was founded was Dr. Trask, twenty-nine, then Dr. Kellogg, forty, and Dr. Gibbons, forty-one.

John Boardman Trask came to California overland with John W. Audubon, as related before this, and his interests seem to have been perhaps the broadest of any of the seven founders. It was doubtless to Dr. Trask that each of the Academy members turned for that sympathetic interest in the individual special studies that so often isolate members of a scientific society. Perhaps Trask's particular interest was that of the potential use of native plants for medicinal purposes. R. E. C. Stearns, who knew him as a close friend, spoke of Trask's "genial qualities, untiring energy and all-around ability" and said that he was "the leader, closely followed by Dr. Albert Kellogg." Complementing the gentleness of Kellogg, Trask's calm assurance in the face of difficulties must have been a staying power in the survival of the Academy during its insecure years. John Xantus, when in San Francisco on his way to Lower California for birds for Baird and plants for Gray, wrote to Baird at Washington that "Dr. Trask is particularly kind to me, and so is Dr. Ayres, who both told me to consider their houses as my own, and command their services no matter how."

Dr. Henry Gibbons, the first of four generations of physicians, was particularly interested in meteorology and kept weather records of such accuracy that the Smithsonian Institution was happy to publish them.

Naturalists in California After 1853

Born in New Hartford, Connecticut, educated in medicine at Charleston, South Carolina, and Transylvania College, Lexington, Kentucky, Albert Kellogg came to California in 1849 and evidently first engaged in business. He had practiced in the South but those who knew him say he was never known to request a payment. Never blessed with a strong constitution, Dr. Kellogg returned to his New England home and soon joined a party bound for California by way of the Horn. He arrived at Sacramento on August 8, 1849. The plant collections he had made along the west coast of South America at ports of call were destroyed in a flood at Sacramento soon after his arrival. He was associated in Sacramento with the Connecticut Mining and Trading Company, but removed to San Francisco about the year of the Academy's founding and established a pharmacy business there with some medical practice on the side. He entered into the spirit of the Academy from its very inception, and seems to have especially stimulated the members and visitors to the city to communicate specimens to the Academy for study and identification. One of the most prominent of these participants was Dr. John A. Veatch, of whom we shall have more to tell directly. Dr. Kellogg's personal botanizing began in earnest in the summer of 1867 when he accompanied Professor George Davidson of the United States Coast Survey and W. G. W. Harford to Alaska. Several hundred species were collected in triplicate, one specimen going to the National Herbarium at Washington, one to the Philadelphia Academy, and one remaining in the growing collection of the Academy. George Davidson described this Alaskan trip thus:

> We lived in the same contracted temporary deck cabin for four or five months under many trials and inconveniences, and the sweetness of [Kellogg's] character was as pervading and refreshing as the beauty and fragrance of the flowers he gathered. . . . He was completely absorbed in his duties; he knew no cessation to the labor of collection and preservation; his genial nature attracted assistance from every one, and all learned to admire and to love him.

Davidson continues:

> [Kellogg] worked for the [Academy] and believed in its success when the number of members could have been counted on one's fingers, and when the means of supporting such an institution and publishing its results came wholly from their professional earnings.

From 1867 to 1870 Dr. Kellogg visited localities from Donner and Cisco to Ukiah, Red Mountain, Cahto, and Santa Cruz Island. Some of his local trips recall the days when the geography of California was quite different from today: "Lobos Creek, near San Francisco"! These collections often, though not always, carried collection numbers but a new series was evidently initiated every year. His last decade was pretty constantly spent drawing trees and shrubs. More than four hundred of these drawings "including all the oaks, all the coniferous trees, poplars, many of the willows and ceanothi, dogwoods, and many herbaceous species" were left with his friends, Dr. W. P. Gibbons and Mr. Harford, to be disposed of as they might think best. The oak drawings were published with commentary by Professor E. L. Greene as *West American Oaks,* under a subvention from Captain James Monroe McDonald, 1825–1907, pioneer capitalist and philanthropist. Captain McDonald was one of the three donors of the Rickseeker Collection of Coleoptera to the University of California in 1881. Kellogg's drawings showed "the very faithfulness of detail with the taste of an artist," yet "the botanist may rely upon the scrupulous exactness of every minute line and dot." Kellogg would not have claimed the rank of scientific botanist but rather a nature lover in the true and full sense. Kellogg lived in the early years at San Francisco with Harford in a small place on Telegraph Hill where they kept "batchelor's hall." He never married and died at the home of his very dear friend Harford in Oakland in 1887. William H. Brewer tersely summarized his rôle when he wrote, "no name is more intimately associated with the botany of the state during this period" than Kellogg's.

John Allen Veatch was one of those early collectors whose specimens engaged Kellogg's attention. Veatch lived in Texas from 1836 until 1845, during which years he had met the enthusiastic botanical collector, Charles Wright. Veatch left a wife and five children in Texas to join the Gold Rush, and when his wife Ann failed to hear from her husband as the months stretched into years she filed a petition for divorce on the grounds of continued abandonment. It is not certain just when Veatch first got in touch with the Academy but in 1855 he was elected a corresponding member and he later served as Curator of Conchology. During these years Dr. Veatch—for he had certified for practice in the custom of those days—traveled from Red Bluff to the Salton Sea, where he carefully inspected the mud volcanoes and wrote his observations. In 1858 Veatch was on Cedros Island [written "Cerros Island" in contemporary accounts], where he was preceded only by the surgeon aboard H.M.S. *Herald,* Mr. J. Goodridge. Veatch's collections were by far the most extensive yet made on the island, though often scrappy specimens by our standards, and Dr. Kellogg published his discoveries in the San Francisco weekly *The Hesperian*, illustrating many of his novelties with drawings. Kellogg's poetic soul is laid bare in the vernacular names that he gave the new species. One of Veatch's plants appeared, for example, as the "hummingbird's dinner horn." Kellogg's scientific names were not infrequently hyphenated words of curious construction that some botanists felt obliged later to edit or disregard altogether.

Though not a "founder" in the strict sense of being present at the meeting of April 4, Dr. H. H. Behr joined the Academy on February 4, 1854, to launch a lifetime of service to the young organization. Dr. Behr was thirty-six when he joined the Academy; he was born at Colthen, Duchy of Anhalt, Germany, and took his medical degree in Berlin in 1843. His coming to the feverish San Francisco of 1850 was the outcome of his participation in the Revolution of 1848. In temperament, then, Behr easily adjusted to the rough manners of the frontier city, and took up practice at once. But he allowed plenty of time to collect plants and these he sent to Hamburg, St. Petersburg, and elsewhere. Fortunately Dr. Behr has narrated his experiences of these early years in an article entitled "Botanical Reminiscences of San Francisco" (*Erythea,* 4:168–173, 1896). Behr's copy of Endlicher's *Genera plantarum* was the chief resource for the study of the troublesome specimens that were brought to the Academy at this time. He taught classes at the California College of Pharmacy and prepared his *Flora of San Francisco,* a rare book today, for the use of the pupils. But Behr's interests were much broader than botany alone. He wrote poetry, humor, and travelogues—his account of two years spent in the Philippine Islands appeared in the *Atlantic Monthly*. His writings were warmly acclaimed in Germany. It is natural that his spiritual link was with Alexander von Humboldt, Schlechtendahl, Ferdinand von Mueller, Hillebrand, Louis Agassiz, and Max Müller. Those who came to San Francisco from afar were sure to find Dr. Behr a hearty host, and it would be difficult to know how important was his influence in the lives of the many scientists and others that he chanced to meet. A man of good will and generous spirit, he died at the age of eighty-six at his home at 1215 Bush Street, in the city with which he had been identified for fifty-four years.

Dr. William Peters Gibbons had taken his M.D. degree in 1846 and sailed from New York in 1852 for California via Panama. While crossing the Isthmus he fell a victim to cholera and would likely have perished there, had not W. C. Ralston carried him in his arms aboard the vessel bound for San Francisco. This is the Ralston who later directed the Bank of California, was a steamship owner, and enterprising capitalist. Dr. Gibbons arrived in San Francisco in January, 1853, and at once began to practice medicine in the city. Quite certainly he met Dr. Behr early that year, as well as Dr. Kellogg. He became active, not only in the Academy, but in the California State Medical Society as well, serving as chairman of the committee on medical botany and as a contributor to its *Transactions*. He was particularly interested in fishes and J. G. Cooper named the genus *Gibbonsia* in his honor. Dr. Gibbons was the son of William Gibbons (1781–1845), Quaker physician and friend of the Pennsylvania botanist, Dr. William Darlington. W. P. Gibbons collected plants in California at least as late as 1874, as represented by sheets in the Torrey Herbarium. He mentions making an herbarium on one occasion but whether this fell to the Academy and in 1906 to destruction I do not know. From 1863 until his death at the age of eighty-five Gibbons was a resident of Alameda. We will quote from his writings later in our chronicle when he considers the State Geological Survey.

Hiram G. Bloomer first set out for California in 1849 but had to turn back on reaching Panama because of sickness; he tried again, successfully, in 1850. I have no information on his principal occupation but he was devoted to botany from the first of his California residence, and participated in the life of San Francisco, serving as a member of the Committee of Vigilance and of the Fire Department. He was active, too, in the Lincoln presidential campaign. He was generous in presenting books to the Academy's library in its early years. It is important to recognize that Bloomer introduced James Lick, the philanthropist, to the needs of the Academy. It will be remembered that the Academy built new quarters on Market between Fourth and Fifth streets in 1891 upon property deeded to it by James Lick. Lick also made the Academy one of two residuary legatees, to receive one half of his estate after all other bequests had been paid. Bloomer's botanical interests centered around the Liliaceae, and he grew many of the native species in his garden. Kellogg named a flower found by Dr. Veatch at New Idria *Bloomeria* in Bloomer's honor. Bloomer's herbarium of several thousand sheets was evidently lost soon after its presentation to the Academy but duplicates had been sent to Asa Gray and others during the State Survey period.

William G. W. Harford was one of those Academy members who could be expected at every meeting. "Six feet in height, of a Lincolnian gauntness, with a pioneer style of luxuriant beard and bushy eyebrows," he was even more shy and retiring than his friend, Kellogg. Like Kellogg, he was of a simple manner, of a deeply religious nature, and devoted to the beautiful. Conchology was perhaps Harford's special interest, and he served as the Academy's curator in that field in 1867, 1868, 1874, and 1875. He was Director of the Academy from 1876 to 1886. Spiders and beetles also interested Harford, along with botany. He and Kellogg made up sets of Oregon and California plant collections in 1868 and 1869 and these reached the herbaria of Europe, as well as the herbaria of Englemann, Torrey, and Gray. Greene and Parry dedicated the polygonaceous genus, *Harfordia,* to his memory in 1886. He was a close associate of George Davidson, with whom he traveled to Alaska in 1867 as naturalist on the United States Coast Survey. Like so many of his cronies at the Academy, Harford lived to be an octogenarian.

Colonel Leander Ransom was an engineer before he came to California by sea in 1852. He was then fifty-three years of age, and had served the previous thirteen years as President of the Public Works of Ohio. He was sent to California by the Federal Government to establish a United States Surveyor General's office in San Francisco and, finding the city to his liking, he became a permanent resident. Always interested in geography and land forms, he is remembered for establishing two of the most important meridian lines on the North American continent, the Mount Diablo base and meridian lines, on July 17, 1851. For many years Colonel Ransom served as the Academy's president, and Dr. Kellogg remembered him in the name of a native oak, but *Quercus Ransomi* is hard to find today even in the synonymies of the oaks!

Three botanical explorers, Archibald Menzies, David Douglas, and John Jeffrey, were born only a few miles apart, in the county of Perth, in England. The last of the trio, John Jeffrey, collected plants and seeds in northern California and Oregon during 1852–1853, sponsored by the "Oregon Committee" of Edinburgh, which had raised money by subscription for what is generally called the "Oregon Expedition." Each member was to receive a portion of the seeds collected. Jeffrey was chosen and contracted to keep a diary on the trip, but no seeds ever reached Scotland. Of perhaps ten boxes of seeds and specimens sent, five reached England but they contained relatively few herbarium collections. Jeffrey botanized in the Salmon River Mountains and on the south slope of Mount Shasta, and reached San Francisco on October 7. He was ill in San Francisco that winter, and did not write his sponsors in Edinburgh or even call for his mail at the British Consulate. Mr. William Murray, of Henderland, who was in San Francisco during the fall of 1853, and Andrew Murray, brother of the secretary of the Committee, could not locate Jeffrey in the city. Jeffrey, perhaps through a friend, dispatched a final small box of tree seeds early in January of 1854. Sometime in the spring of that year Jeffrey is said to have left with an American party for Yuma, with the intention of collecting on the Colorado Desert. He was never heard from again and only conjectures surround his death. "Bearing in mind that Menzies and Douglas went to a virgin country, [Jeffrey's] collections [after them] do him no discredit, even as compared with theirs."

Jeffrey's unfinished work was carried on by William Murray, accompanied by A. F. Beardsley, "a gentleman from whose energy and knowledge of the mode of life in the regions they traversed, he derived much assistance." They collected conifers, so much in demand in British gardens, in the Sierra Nevada, including *Pinus Beardsleyi,* later considered a synonym of *Pinus ponderosa.* Beardsley visited the Santa Lucia range in 1856 for seeds of *Abies venusta,* which had been recently introduced into England by William Lobb. But evidently neither Murray nor Beardsley were employees of Peter Lawson and Company, Scottish seedsmen. William H. Brewer, who reenters our chronicle later, met Beardsley in October, 1861, at a tavern in Napa Valley whence Brewer, then with the State Geological Survey, had repaired "to read the news." Brewer says:

> While there, a rough but intelligent looking man entered into conversation and invited me to his house a few rods distant for a "glass of *good* cider." I went, got the cider, the best I have tasted in the state, and went into his house. I found him an intelligent man, quite a botanist, and even found that he had some rare and expensive illustrated botanical works, such as *Silva Americana,* worth sixty to eighty dollars—the last place in the world I would have looked for such works. He does not own the ranch, is merely a hired man, having charge! There is an orchard of ten or twelve thousand trees and a vineyard—he makes wine and cider and sells fruit.

Brewer returned the next day for more cider:

> Mr. Beardsley came to camp and invited us to his house for more cider. We went, spent an hour, when it cleared up, and we started for a peak seven or eight miles northeast.

Just as Douglas and Jeffrey collected seeds and plants in California for English horticulture, William Lobb spent seventeen years with the nursery firm of James Veitch of Exeter, going first to South America to collect orchids and new plants for the "stoves." Lobb reached San Francisco in the hectic summer of 1849 but he turned from the lure of the bonanza road to complete immediate plans for the exploration of southern California! His first season included a trip into the Santa Lucia Mountains, whence he was able to introduce the bristle-cone fir successfully into England. During the spring of 1850 Lobb was joined by Dr. C. C. Parry, then sojourning in Monterey, on a trip south at least as far as Mission San Antonio de Padua. The 1851 season he spent north of San Francisco, and in the following year he reached the Columbia River, collecting all the while. Perhaps it was during the winter of 1852–1853 that he learned of the fabulous "Big Tree" through the testimony of a hunter, Mr. Dowd by name. In any event, Lobb set off directly for the Calaveras Grove early in 1853 and, finding the trees and collecting the foliage, cones, and seeds, hastened back to England as the *scientific* herald of the greatest tree on earth. The apogee of Lobb's career came perhaps, not in California, where he was hardly known, but at Sydenham at the exposition put on in 1857 in the Crystal Palace! There a section of a Big Tree was exhibited, standing 116 feet high—as high as the bark had been stripped from a living tree—in all its majesty, bearing the name *Wellingtonia* which had been given it in December, 1853, by England's excellent botanist, Professor John Lindley. Some saw in it proof again that Britain was still the general in the vanguard of discovery, with *Wellingtonia* her latest conquest! It was called the "Mammoth Tree," and public interest ran high on both sides of the Atlantic, although Americans were not a little piqued at the "scoop"! But history takes some sharp and unexpected turns. A decade later William Lobb was lowered into an unmarked grave in the Public Lot at Laurel Hill cemetery, deserted and forgotten, a victim of paralysis at fifty-five.[2] If we are to believe Parry's report, Dr. Kellogg thought that Lobb took unwarranted license with the information that he had wrested from Mr. Dowd. But though William Lobb did first make known the Big Tree in a formal way, the American name, *Sequoia,* has found a secure place in our literature and language.[3]

Julius Froebel and H. H. Behr were both "Forty-eighters," that is, members of the "group of German idealists who fought to establish a liberal and unified Germany and then came to the United States as refugees from the reaction." Froebel had founded a radical opposition newspaper, the *Swiss Republican,* in 1839, and subsequently participated in the 1848 Revolution. He was arrested, condemned to death, pardoned, and returned to Switzerland, but he left for America and arrived in New York in 1849. In all, Froebel made four different trips to Central America and the Southwest. It was toward the close of his third trip that he visited San Francisco in the fall of 1854, arriving by coastwise boat from San Pedro. He wrote:

> On the morning of October 3rd, we entered the Golden Gate. Much had I heard of the grand scenery of the Bay of San Francisco, and I can only state that reality surpassed my expectations. . . . Whatever splendid sites of cities other parts of the world may have to boast of, in North America the palm will never be disputed to San Francisco.

Froebel comments further:

> Every European, many Asiatic, and some American languages, meet the ear while

2. Lobb's grave was moved and appropriately marked years later by San Franciscan garden lovers under the aegis of Miss Eastwood.
3. Buchholz's segregate genus *Sequoiadendron* for the Sierran tree as distinct from the coastal redwood happily carries on the historic connotation.

you are walking in the streets. This apparent chaos of heterogeneous elements has been brought together, and is kept in motion, under the great form and system of Americanism, with its restless labour, its ever-active spirit of speculation, and its devotion to utilitarian purposes.

His two-volume narrative *Aus Amerika. Erfahrungen, Reisen und Studien* (1857–1858) was abridged as *Seven Years' Travel in Central America, Northern Mexico, and the Far West of the United States* (1859). He contributed an article on the physical geography of North America, dated "San Francisco, Dec. 8, 1854" to the *Ninth Annual Report of the Smithsonian Institution* (1855).

Emanuel Samuels was sent to California jointly by the Smithsonian Institution, the Boston Society of Natural History, and Academy of Natural Sciences of Philadelphia to collect birds. He arrived in 1855 and most of his collections were made in the vicinity of Petaluma. What relation, if any, Emanuel Samuels may have borne to "Rev. Mr. Samuels" mentioned by Sereno Watson when he described *Chorizanthe valida* collected at the Russian Colony in Sonoma County I have not been able to determine.

General Amos Beebe Eaton, the father of the distinguished Professor of Botany at Yale, Daniel Cady Eaton, collected a few ferns about Carquinez Strait in 1855.

January 27, 1855, saw the completion of the Panama Railroad from Panama City on the Pacific to Navy Bay, or Aspinwall, on the Atlantic. Its construction had employed in all some seven thousand men drawn from all over the world, some from the mines of California a few years before. Daily service was established both ways, the fare for adults being set at $25. The running time at first was from five to six hours but was later cut to three hours, with as many as fifteen hundred passengers carried in a single half-day. And, you will be right when you predict: most of the passengers were en route to California!

Coming by boat from across the Pacific, Ezechiel Jules Remy, French naturalist and explorer, traveled under the nominal auspices of the Natural History Museum of Paris. Remy had been collecting in the Hawaiian Islands intermittently between 1851 and 1855 before he arrived in San Francisco in the summer accompanied by the Reverend Julius Brenchley. Brenchley will be remembered for his placing a plaque at the site of David Douglas' grave on the island of Hawaii. Remy and Brenchley left San Francisco on July 18, 1855, for Salt Lake City via Carson Valley. From their extended visit in the Mormon city they published an illustrated two-volume account of the geographic and social features of the community. Leaving on October 26 Remy traversed the Great Basin to St. George and went on to Las Vegas and Los Angeles, which he reached November 29. Returning to San Francisco, Remy took passage for Central America. Parry refers briefly to Remy's few plant collections reaching the Natural History Museum at Paris.

Thomas Bridges, British naturalist and horticultural collector, a Fellow of the Linnaean and Zoological societies of London, had been in South America before coming to San Francisco in November, 1856. There is substantial evidence that he was an enthusiastic collector and he proved to be California's first resident ornithologist. One obituary noted that "few, if any, more useful lives have passed away as martyrs to science during the present century." Bridges' principal field of collecting was the Sierra Nevada. There he collected seventy-five bulbs of the lily, *Lilium washingtonianum,* for his English employer but the steamer *Central America,* which carried them, was lost at sea. He wrote W. J. Hooker that he was going to make an effort to replace them. Evidently he visited the Academy often, and in 1858 he wrote Hooker of his pleasure at finding Beechey's *Voyage,* Torrey's works, and other books in the Academy's library. He lived in "Chinese House" on Eleventh Street between Market and Mission streets, and may have associated with William Lobb, then a resident of the city, but of that friendship we have no hint. One of Bridges' most profitable trips was to the mining town of Silver Mountain on the east slope of the Sierra Nevada near Ebbetts Pass in 1863. There he met William H. Brewer and Brewer wrote:

> It was a relief to meet Mr. Bridges, an old rambler and botanical collector, well known to all botanists. . . . It was a relief to meet him and talk botany; yet, even he is affected—he has dropped botany and is here speculating in mines. "Mining fever" is a terrible epidemic; when it is really in a community, lucky is the man who is not affected by it. Yet a *few* become immensely rich.

In April, 1865, Bridges set out on a collecting trip to Nicaragua but was stricken with malaria and died at sea, September 9, 1865, en route back to San Francisco on the steamer *Moses Taylor.* Captan Blethen, Bridges' friend, brought his body to San Francisco and he was carried to the *ultima thule* of the city, Lone Mountain Cemetery.

One of the most colorful figures in the history of California's progress in science was Andrew Jackson Grayson. Born at the Grayson cotton plantation on the Ouachita River in northern Louisiana, August 20, 1819, he traveled widely, won and lost, and died three days short of his fiftieth birthday at the Mexican port of San Blas. Grayson made the overland trip from Independence, Missouri, in 1846, with his young wife and child, and reached California in October. The Donner party traveled with them as far as Fort Bridger, when the emigrants separated, the Donner party pushing on to tragic death, the Graysons to some considerable fortune in the "diggins," followed by a less fortunate venture into the mercantile business. Finally Grayson tried his hand at trapping, and it was during this period, when he occasionally visited the Mercantile Library in San Francisco, that he chanced upon Audubon's *Birds of America.* He was so deeply thrilled with the paintings that he determined to match them for the birds of the Pacific slope. So ardently did he adopt Audubon's flamboyant style, sketching the birds in stiff or unnatural postures, that he quite aptly may be called the "Audubon of the Pacific." Grayson also gave his bird portraits backgrounds of quite accurate, if occasionally mixed, delineations of the native plants. From 1855 to 1857 Grayson made sketches of the birds about San Jose and the Napa Valley, and in 1857 sailed for Tehuantepec on the *Mary Taylor.* But his plan to include the Mexican fauna in his opus was dealt a blow by the wreck of the schooner in the bay of Ventosa, when his books, drawings, paper stock, and colors were ruined. Penniless, he took up a job as surveyor to recover his funds, but he found drawing paper impossible to procure and he turned to the preparation of bird skins. Some of these reached S. F. Baird, who was most enthusiastic about them. After a visit to San Francisco, Grayson returned to Mexico in company with J. M. Hutchings, of "Yo-Semite Valley" fame, determined to settle at Mazatlan and sketch the local birds for his book. During this period he wrote travel articles for the *Overland Monthly* and the press. John Xantus was his correspondent at Cape San Lucas. A hearing was effected with Emperor Maximilian and Empress Carlotta but the collapse of their régime brought an early end to Grayson's support for a projected *Birds of Western Mexico.* It was while on an expedition to Isabel Islands for nesting sea birds that he was taken sick with the "coast fever." The journal *Condor* has been currently publishing his beautiful drawings of Mexican birds. Grayson's notes for many of these will be found in Bryant's article published in *Zoe* for April, 1891.

Robert Edward Carter Stearns came to San Francisco in 1858 at the age of thirty-one to become a partner in the large printing establishment of his brother-in-law. This firm published the influential *Pacific Methodist* and, in the absence of the editor, Stearns took over. This journal was instrumental in keeping California in the Union during the Civil War. Always interested in zoology, Stearns made a trip to Florida in 1863 for invertebrate collections for the Smithsonian Institution. In the *Proceedings* of the Academy for 1868 Stearns treated the mollusks of Bolinas Bay. The University of California made important advances under President Gilman, and during this period Stearns served as secretary to the University, beginning in 1874. He launched a plan for developing the plantings on the campus in 1882 which was carried forward by Professor Greene when he came in 1885. In turn Stearns was U. S. Fish Commissioner, paleontologist under John Wesley Powell, and assistant curator of mollusks under S. F. Baird at the Smithsonian. Stearns often contributed articles on marine life to Charles Russell Orcutt's *West American Scientist,* as well as to Brandegee's *Zoe.* Through the years away from California Stearns kept in touch with his friends Trask, Kellogg, Harford, Dr. Wesley Newcomb, and others at the Academy.

Particularly interesting was Dr. Newcomb's cabinet of shells. Josiah Whitney remarked in a letter to his brother Will on June 2, 1862, that he had examined Newcomb's "superb collection of shells—one of the best in the country, especially in the department of land shells. He has in all between 10,000 and 11,000 species." Stearns and Newcomb were brought into close friendship by their common interest in conchology and it was a bitter loss to Stearns on his return to California in 1892, to learn of Newcomb's death. Newcomb had been a practicing physician in the Hawaiian Islands for five years and had become an authority on the land shells of the islands.

It was in 1859 that Dr. Veatch set out for Cedros Island to verify the rumors of mineral wealth there. Whalers, seal hunters, and fishermen visited Sebastian Viscaiño Bay and brought out wealth in furs and oil, but few persons paid much attention to the volcanic soil itself. Since there was a high point on the island which might yield plants characteristic of northern latitudes, Dr. Veatch was eager to examine its flora. He brought back only about two dozen specimens for Dr. Kellogg to study, but they proved almost without exception to be undescribed! Of course one of them became *Veatchia!*

In 1859 Louis Agassiz' son, Alexander Agassiz, twenty-four, came to San Francisco to take a position with the Coast Survey as engineer to survey the Gulf of Georgia and was assigned to the *Fauntleroy.* Returning to the city, Agassiz applied himself to the medusae and viviparous "perch" (Embiotocidae) of San Francisco harbor, making drawings and notes for his father. Alexander Agassiz later invested over a million dollars, made in the Calumet and Hecla

Copper Mine on Lake Superior, in Harvard's Museum of Comparative Zoology, which his father had founded. "The Bismarck of American Science," "fearless, resolute, quick to anger, definitely purposeful and full of resource," Alexander proved a "colossal leader of great enterprises, fully as much as he was a man of science."

The California State Legislature created the office of State Geologist and authorized a geological survey of the State on April 21, 1860. Josiah Whitney was selected as State Geologist and William Henry Brewer, Botanist. Rather later, J. G. Cooper was prominent as a zoologist. William More Gabb joined the Survey in 1862 as paleontologist, and was described in Brewer's words as "young, grassy green, but decidedly smart and well posted in his department." Thus just seven years to the month came the second *organized* institution for the promotion of natural sciences on the Pacific Coast. It was fortunate, too, that Whitney and Brewer were destined to work together on this survey for they proved a well matched team.

Whitney was forty-one when he took over the leadership of California's geological survey. Schooled at the Round Hill School, founded at Northampton, Massachusetts, by George Bancroft and J. G. Cogswell, and subsequently at Yale under Benjamin Silliman, whose chemistry lectures excited him, Whitney managed the Iowa Geological Survey before taking over the California job. The State Survey proceeded well enough at first, but met with little sympathy from the legislature after it failed to lead a waning mining industry to a new bonanza at home and halt the loss of men to the Pikes Peak gold rush. But Whitney was thorough in his prosecution of the Survey and by the end of the first year of his work he had already visited forty of the then forty-six counties of the State. Brewer, his first assistant, had traveled 2,600 miles on muleback, a thousand more on foot. The age of the auriferous gravels had been determined as Jurassic; the coal of the Coast Ranges, Cretaceous; about two hundred species of fossils had been discovered and a "great many new animals and plants." In the personal sense Whitney was less the State Geologist to his scientific associates "than the gay Apothecarius of Clover Den. He was kindly, just, unsparing of himself; and his associates gave him not merely esteem but affection." Dr. Trask turned over his geology notes and fossil collection for the use of the Survey but Brewer found Blake "distinctly less friendly." Whitney was influential in the life of the Academy and in matters of publications was ever a driver for accuracy and thoroughness. In a letter to his brother, William Dwight Whitney, he reported:

> . . . of late I have been much engaged with the the affairs of the California Academy, as we have had to move into and fit up new rooms [this was January, 1867], and have tried to resuscitate in general. We seem now to be in a fair way to live; but when I came back last year, it seemed as if it was as dead as a doornail. We have now a pleasant reading room with a goodly number of scientific periodicals; and we are fitting up our meeting room and collections in a respectable manner. The last sheets of the Proceedings . . . will tell you what we have been doing, and you will notice my account of the [Calaveras] skull, etc.

But the State Survey issued only three of its final reports, the other volumes being published through outside resources, including Whitney's personal funds. Brewer brought out the botany volume by means of a $5,000 private subscription, "engineered by Judge S. C. Hastings of San Francisco and helped on by Gilman, Leland Stanford, and D. O. Mills," with "Whitney's help." But it cost Brewer "two years' unpaid labor, $2,000 of [my] pocket, and the accompanying loss of [my] salary at Yale." The botany volume sold to the public for four dollars. The three volumes on birds were printed largely at the expense of Alexander Agassiz, with Baird contributing a thousand dollars on his portion. The geological materials were published largely through the "M.C.Z." of Cambridge: "the gravel volume will form one of the Memoirs of the Zoological Museum."

Whitney stayed on with the State Survey until 1874, the next year taking the Sturgis-Hooper Professorship of Geology at Harvard, which he held until his death in 1896. "Honors did not come to him as abundantly as to many perhaps less worthy," concludes the historian of geology, G. P. Merrill. Some strong-worded opposition to the State Survey came even from scientists. Dr. William P. Gibbons wrote in the *Overland Monthly:*

> . . . as to any report on botany, or any collection of California plants, three sets have been made up: one for the California Academy of Sciences; one for the University of California; while one has been sent out of the State, and eastern botanists have the credit of devoting their time to working it up, in occasional paroxysms, without remuneration. It would have been far better for the interests of the State and of science had this [California Geological] commission never existed.

Dr. Gibbons evinced more local pride than imagination when he said:

> California scientists would have accomplished more work, without aid from the State, than has thus far, to all practical purposes, been achieved by the commission.

Gibbons' assessment appeared in August, 1875. The first volume of the "Botany Report" was published the following year, and the second volume, in a necessarily smaller edition, four years later. Kellogg, Bolander, Behr, and perhaps a few others, might have eventually described the greater part of the California flora, but the number of avoidable synonyms may well have increased thereby because of the inability of the resident botanists to check against the existing specimens in Eastern herbaria.

Thirty-two-year-old William Henry Brewer accompanied Whitney and his family from Massachusetts to California via Aspinwall. When the party stepped ashore from the *Golden Age* on November 14, 1860, they were greeted by Mr. S. Osgood Putnam, of the California Steam Navigation Company, who had backed the State Survey appropriation in the legislature. Brewer had finished at the Sheffield Scientific School at Yale in 1852—a member of its first class—and had studied abroad under the chemists Liebig and Bunsen. Along the academic way he had acquired a lively taste for botany and a near dead-shot judgment in geology. He had applied for a post on Captain Gunnison's expedition but had been turned down; Gunnison and his party, it will be remembered, were massacred by a band of Indians in Utah. Brewer was "fond of travel, not for rest, but for the recreation which he found in careful observation and record of facts in all departments of human interest." No botanical collector in California up to his time made as careful field tickets as did Brewer; fortunately, too, his field book is preserved at the Gray Herbarium. His journal, edited by F. P. Farquhar and first published in 1930 under the title *Up and Down California in 1860–1864,* is a rich but unscheduled dividend of the State Survey!

William More Gabb of Philadelphia was the same age as Brewer when he joined the State Survey but there the likeness breaks, for hardly could two men have been more contrasting: where Brewer was modest, Gabb was bumptious; Brewer was resilient in the face of inevitable adjustment, Gabb, reluctant. Gabb came as an acknowledged authority on Cretaceous fossils. He is described as a "distinctly loquacious person." Brewer was pleased when the serious, unbending Dr. J. G. Cooper saw fit to name a new species of brachiopod *Lingula gabbii!* A close friend of Gabb's in Philadelphia was George H. Horn, the entomologist, who came to California the next year.

Dr. George Henry Horn came to Camp Independence in Owens Valley in 1862, as a member of the Survey, after graduating from "Penn" the year before. But the doctor soon turned from medicine to beetles, a field in which he became a recognized authority. While in California Dr. Horn collected actively about Fort Tejon, Fort Yuma, Surprise Valley, Warner's Ranch, and many other localities. He occasionally made plant collections, particularly in the Owens Valley, and these may be found cited in the "Botany Report" of the Survey. The year 1862 brought the establishment of the Department of Entomology at the Academy, with Dr. Behr as Curator. He served first for five years and then a second term from 1881 until 1904.

A little known figure of this period was Dr. Charles Austin Stivers, U. S. Army, who interested himself in collecting plants about the post in Mariposa County. He brought his specimens to Dr. Kellogg and among them was the remarkable endemic lupine which bears his name today. There is a record of Dr. Stivers' interest in marine algae, too.

The Prussian expedition to East Asia in 1860–1862 had as its geologist and geographer Freiherr Ferdinand Paul Wilhelm von Richthofen. When the expedition set out on its return voyage to Germany from China in 1862, Baron Richthofen parted from the corps and sailed for San Francisco. He arrived in California, "a modest, sincere, affectionate" man about thirty years old, intent on studying volcanic phenomena. Having some private means, he worked only intermittently for the State Survey in those fields that appealed to him. But for Whitney he had a "worshipful admiration," and the two geologists fitted as neatly as pick-head and tool handle. It was Whitney who conceived the idea of a geological survey for China and, indeed, the China survey was planned by the two men on New Year's Eve of 1868. During the subsequent years in China Richthofen wrote long letters to Whitney, which Whitney edited and transmitted to the American Academy of Arts and Letters at Boston for publication. Richthofen evidently made some botanical collections in California, but it is difficult to discover the extent or the destiny of them. He returned to Germany after twelve years of travel to teach first at Berlin, then at Bonn, Leipzig, and finally again at Berlin. From the clues I have seen the as yet unwritten biography of "Life and Times of Baron Richthofen" could be a warm and gracious tale.

Behr's friend, Dr. William Hillebrand, went to the Hawaiian Islands in 1844 for his health, stayed twenty-eight years and identified himself as the leading authority on the flora of the islands. He visited California in 1863 and made some collections about the Yosemite Valley, Big Tree grove, and Mount Dana, as a part of the State Survey.

Brewer mentions William Holden's collecting about a hundred species of plants in the vicinity of Oakland in 1863. These were included in the State Survey, but Holden evidently did not continue his scientific interests.

English-born Shakespearean tragedian, Henry Edwards, traveled with a theatrical company from Australia to Peru and California in 1853, and wrote of his impressions in a slender volume called *A Mingled Yarn* (1883). In 1865 Edwards came back to San Francisco and was associated with the old California Theatre. During all these years on the stage, traveling and as a San Franciscan, he collected butterflies at every opportunity. His collection grew by his own takes and through exchanges until it was one of the finest ever assembled in this country, numbering some 250,000 specimens. In addition, Edwards found time to collect beetles, plants, and shells for his friends in the Academy, of which he was a faithful associate. There and at the Bohemian Club he found a congenial friend in Dr. Behr. Edwards made plant collections at Sausalito, in March, 1877; Summit, on the Central Pacific Railroad, July, 1877; Knights Valley and Skaggs Springs, Sonoma County, in 1877, and in Santa Clara Valley—all of these are represented in the harbarium of the New York Botanical Garden. There's a hint of the actor in his locality on one label "San Leander"!

John Torrey, the senior associate of Asa Gray in midcentury botany, visited California on two occasions. His trip of 1865, made via the Isthmian passage, included a short stay in San Francisco, but he took the Revenue steamer *Shubrick* for Santa Barbara on business for the U. S. Treasury as inspector of banks. Writing in his usual buoyant mood, he told Asa Gray that he was "high admiral of the expedition." He made sure to save some time from the inspection of ledgers and balances to devote to the plants growing around the towns visited: from Borax Lake and vicinity to Donner Lake, Bear Mountain, and the Yosemite.

One of the collectors well known to Torrey and Gray for his valued specimens was Dr. Charles Lewis Anderson, who moved from Minneapolis in 1862 to Carson City, Nevada, and four years later to Santa Cruz. At Santa Cruz his name became synonymous with natural history since there for forty years Dr. Anderson engaged, not in botanical, zoological, and geological investigations for himself, but generously answered various questions for others. In botany he devoted himself especially to marine algae about the bay, to grasses in the hills and valleys of the county, and the willow species along the stream courses.

Edward Tuckerman was a genial, if meticulous, professor at Amherst, and one of the students there in the 1850's was George Lincoln Goodale. Goodale took the medical degree at both Harvard and Bowdoin, and then set up practice at Portland, Maine. From all of this close application his health broke and the year 1865 found him in California trying to find a cure in tramping the hills and collecting the plants about which Professor Tuckerman had talked back at Amherst. The cure must have been complete, and more and more botany supplanted medicine until he settled as Curator of the Botanical Museum at Harvard and for thirty years taught and studied the economic plant collections that came to him. He is remembered as one of the first professors to use lantern slides to illustrate his lectures. Goodale possessed a fine historical sense, too, and preserved mementoes of our botanical past for Harvard's "glory hole," as Thomas Barbour would say.

Less honored but perhaps more influential was the author of the botany best seller that sold 800,000 copies, Professor Alphonso Wood. First a student of theology, then a practicing civil engineer, a teacher of Latin and natural history in the Kimball Union Academy near Hanover, Alphonso Wood found it difficult to teach botany to students from the existing texts prepared by Professor Asa Gray and ventured to discuss the matter with him. Wood suggested that Gray prepare a text better suited to the secondary schools, but the titular head of botany in this country denied the need was a valid one. Professor Wood approached Gray a second time but was again refused, whereupon he set out to prepare a "Class book of Botany" of his own. The first edition of Wood's *Class-book* appeared in 1845 in an edition of 1,500 copies and met with some considerable success. Those faithful to Gray disparaged Wood's intrusion on Gray's established precincts, bolstering their opposition chiefly with the premise that Professor Wood was ill-trained and had an inadequate background to undertake the text. But the *Class-book* was accepted more and more widely among the academies and Wood kept pace with the trend by widening the scope of the text with each new printing until in 1855—only ten years after its first publication—forty-one such "editions" had been issued! With ambition reminiscent of that other challenging professor, Amos Eaton, Alphonso Wood determined to extend his book to include the growing frontiers of America. So he made field trips to Ohio and into the southern states, and in 1865–1866 to the Pacific Coast. It is unfortunate that the details of his Western journey have not survived; suffice to say that he traveled from San Diego to Oregon. Plagued with poor health, limited funds, and the general insecurity attendant on the Civil War, he found it difficult to make headway in his chosen field, but he devoted his last years to botany from the year of his settling at West Farms, New York. The student of California history would like to know more of the association of Alphonso Wood with the person he commemorated in the naming of the endemic mariposa of San Diego County, *Calochortus Weedii*. In the tradition of William Young, who contested the field with John and William Bartram in the early years of the nation, and John Linnaeus Shecut, who nettled Stephan Elliott in the description of the botany of the Carolinas, Alphonso Wood stood against Asa Gray, not so much as a serious challenge to the supremacy of the leaders but to remind us of the impossibility of establishing a monopoly in knowledge.

John Gill Lemmon was an ardent Abolitionist and, as in all the events of his lifetime, turned a loyalty into action and enlisted in the Union Army. But he was taken prisoner and placed in the largest and best, if infamously known, of the Confederate military prisons, at Andersonville, Georgia. It was a log stockade of sixteen and a half acres holding within its pickets 31,678 prisoners in the summer of 1864. Corn meal and beans, with a little meat, was the diet; respiratory diseases, diarrhoea, and scurvy were rampant in the ranks. John Lemmon's health was broken but he escaped interment with the 12,912 men left in the National Cemetery there. He went to California as soon as possible, first to Sierra Valley in 1866, and from eight years of tramping the meadows and slopes in pine-scented air regained his health. Meanwhile, he discovered a world of plant life about him and early in his Sierran residence sent some of his specimens to Asa Gray for their names. With Gray's encouraging letters he continued the search, and paused now and then to write homespun letters to the local newspapers on plant lore. It was a high point when in 1876 he met Asa Gray personally. By 1880 Lemmon was devotedly wedded to botany and so it was with a kind of bigamy prevalent among naturalists that he married Sara Allen Plummer of Santa Barbara. They moved to Oakland and set up a botanical establishment at

5985 Telegraph Avenue, more or less completely filling a large frame house with their plants, books, and the kind of enthusiasm that effectively combats the paralysis of poverty, which followed them from the beginning. The house was easily identified by a large wooden sign bearing in capital letters the words "Lemmon Herbarium." Taking every travel opportunity that presented itself the couple managed to reach distant points in Arizona, the Mount Shasta region, and the San Bernardino Mountains of southern California, taking specimens in sets for sale and exchange. With near idolatrous devotion they sent the first specimen to Professor Gray, and as soon as he responded with the identifications they so eagerly awaited they distributed the duplicates, printed up circulars, and sent off scripts to the press of wild potatoes, resurrection ferns, and outsize records of California trees. From 1888 to 1892 Lemmon was botanist to the California State Board of Forestry and during this period published *Pines of the Pacific Slope* and *Cone-bearers of California.* This last duodecimo handbook was a kind of forerunner of the popular pocket guides of today. The Lemmon collection, rich in isotypes and early records, ultimately came to the University of California but the transcription of the data, written hastily on the margins of the newspapers, suffered somewhat in the curating process. It is unfortunate that the specimens lacked original labels bearing Lemmon's own record of the data for some facts may be learned from a comparative study of the labels made at different times in his lifetime. "J. G. Lemmon and wife" (as the labels read in the older herbaria, bearing witness to a marital warmth that they shared in adversity) were self-sacrificing bearers in the caravan of botanical discovery.

Three women who lived in northeastern California and were enthusiastically interested in plant study were Rebecca Merritt Austin, her daughter, Mrs. C. C. Bruce, and Mary E. Pulsifer Ames. Better known to Asa Gray and Eastern botanists than to most at the California Academy, their plant collections and field notes gave the foundation to our knowledge of the vegetation of that region. "R. M. Austin," as she labeled her collections, came with her husband and children to the gold mines of Black Hawk Creek of Plumas County in 1865. There she began collecting plants and other objects of natural history with no thought of the particular value of her "hobby." Early in 1872 John Gill Lemmon, while peddling books in the mining towns of Sierra Valley, visited her. We may imagine Lemmon showed Mrs. Austin Hittell's *Resources of California,* Scott's *Wedge of Gold,* and perhaps Mrs. Clarke's *Teaching of the Ages,* but it would be sport to know if he took orders for Bret Harte's *Luck* and Stoddard's *South Sea Idylls.* But we do know that Lemmon was exultant when he saw Mrs. Austin's specimens displayed in a "cabinet" made from a soap box. Jepson says that "those who knew the exuberant Lemmon will readily credit the story as related by Mrs. Austin" that "he took off his hat and gave three cheers for the woman who was cooking for miners and at the same time trying to study nature under such adverse circumstances." The Austins removed in 1875 to Butterfly Valley and there she carried out her studies on the pitcher plant *Darlingtonia* known to the local residents as the "cobra plant." Mrs. Austin observed that the amount of fluid increased in the pitchers when they were stimulated by the introduction of bits of meat. One of her earliest correspondents was William M. Canby, of Wilmington, Delaware, to whom she wrote no less than twenty letters on the *Darlingtonia* studies. She was also in touch with C. Keck, an Austrian botanist and dealer in natural history specimens, who reported her recent findings in the organ of the Austrian botanical society. About this time Asa Gray mentioned Mrs. Austin's observations in his book *Darwiniana,* and she published a short note in Coulter's *Botanical Gazette* for 1878. That year the Austins moved to Big Meadows, Plumas County, where Canby paid her a visit. But in 1881 they moved again, this time to Modoc County, where she made some of the first collections for the county, alone or in company with her daughter. The pages of *Pittonia* carry frequent mention of the Austin and Bruce collections, some singled out for such recognition as *Scutellaria austinae* and *Collinsia bruceae.*

Comparatively little is known of Mary E. Pulsifer Ames of Auburn, whose plant collections, like those of Mrs. Austin, are occasionally cited in the *Botany of California,* particularly the second volume. She was evidently at one time a resident of Taylorsville, Indian Valley, a correspondent of C. Keck of Austria, as was Mrs. Austin, and a contributor to the *California Horticulturist and Floral Magazine. Astragalus pulsiferae* of Plumas County was named in her memory by Asa Gray. She died at San Jose, at the age of fifty-seven.

Gulian Pickering Rixford, the son of a scythe-maker, born in East Highgate, Vermont, came to San Francisco in 1867. Rixford's real interest was evidently horticulture and applied entomology, but he worked as a journalist "to pay expenses." For eight years he was on the editorial staff of the *Evening Bulletin* and its business manager for thirteen years. An ingenious plan to finance the introduction of the Smyrna fig from Asia Minor was put up to the proprietor of the *Bulletin.* Cuttings were to be distributed to three thousand subscribers to the paper as a sort of premium, and gratis to nurserymen and fruit growers. Seventy thousand cuttings were distributed in 1880 by this device. In April, 1892, Rixford made incidental collections of some interest in Owens Valley of Inyo County, including *Eremolithia Rixfordii,* named by Brandegee. In 1913 Rixford was chosen Director of the Academy and in 1930 awarded the Frank N. Meyer Medal for distinguished services in plant introduction.

English-born Richard Harper Stretch, engineer and entomologist, visited America first in 1861 and finally settled in California in 1867. Educated in Quaker schools abroad and apprenticed to a draper, he became enthusiastic about natural history as a boy. He joined the Academy as a resident member the year he came to California and devoted his time particularly to moths and their taxonomy. Fine drawings of moths executed by him were published in 1874, and later his collection of about five thousand specimens was given to the University of California. Stretch was a close friend of Dr. Behr and of Henry Edwards, following whose death he lost interest in entomology and devoted his time more wholly to engineering. Stretch was the first to call attention in official circles to the presence of the cottony cushion scale in California. He spent his later years in the Puget Sound region.

Of Henry Nicholson Bolander, Asa Gray wrote in 1868 that "for the last few years no one has done so much as Mr. Bolander for developing the botany of his adopted State, and perhaps no one is likely to do so much hereafter." At that time he dedicated the pretty genus *Bolandra* of the Saxifrage family to him. Bolander came to Columbus, Ohio, at the age of fifteen, from Schleuchtern, near Frankfort, Germany, his birthplace. In Columbus he came under the influence of Leo Lesquereux, the bryologist, and from this early contact persisted a life-long interest in mosses. Bolander arrived in San Francisco December 5, 1861, to find the State Survey staff assembled in the city. Dr. Kellogg, and other members of the Academy, became his intimate friends. It is singular that there is not a single mention of Bolander in Brewer's letters, at least in so far as edited by Farquhar. Bolander became State Botanist at the close of the State Survey late in 1864, on the resignation of Brewer. Between 1864 and 1873 Bolander botanized over nearly all parts of the State, his ramblings being exceeded perhaps only by those of Brewer himself: from Ukiah and Red Mountain to Mount Dana, Mono Lake, and south to Cuyamaca Mountains and San Felipe Cañon. Bolander's most serious interest was in grasses, about which he wrote briefly in the Academy's *Proceedings.* Lesquereux wrote in 1869 that Bolander had in less than one year collected as many species of mosses as all the other collectors together. The San Francisco publishing firm of Anton Roman and Company published Bolander's small quarto volume in 1870 entitled *Catalogue of the Plants Growing in the Vicinity of San Francisco, Embracing the Flora within 100 Miles of the City.* Between 1871 and 1875 he served as State Superintendent of Schools, and during this period his botanical activities began to wane. His plant collections were well known in Europe, De Candolle reporting the herbarium at Geneva as containing 1,156 species of his gathering, and his specimens were also received at Kew and Leipzig. His death occurred at Portland, Oregon, August 28, 1897, by which time his name had quite disappeared from current botanical literature.

On the morning of October 21, 1868, a destructive earthquake shook the city of San Francisco. As Bret Harte remarked, "Enough that we know that for the space of forty seconds—some say more—two or three hundred thousand people, dwelling on the Pacific slope, stood in momentary fear of sudden and mysterious death." Bret Harte chastises the citizens for trying to hide the seriousness of the earthquake lest the reports have an unfavorable effect on tourist interest in the city, and adds:

> It is surprising how little we know of the earth we inhabit. Perhaps hereafter we in California will be more respectful of the calm men of science who studied the physique of our country without immediate reference to its mineralogical value. We may yet regret that we snubbed the State Geological Survey because it was impractical.

The earthquake and its economic reverberations threatened the Academy's income at this time, and it was Stearns and Whitney, in particular, who stood behind its survival.

Though not realized at the time, an important stimulus to the promotion of the natural sciences in California at this time was the formal charter granted the University of California on March 23, with Henry Durant installed as its first President. Practically from the beginning the University worked along with the Academy across the Bay in many matters of mutual scientific interest.

An obscure visitor to California at this time was Heinrich Sylvester Theodor Tiling, from Livonia, a physician at the hospital at Sitka, who collected at Unalaska in 1851 and at Sitka between 1866 and 1868. He visited Nevada City about 1869 and collected the type there of *Horkelia Tilingi* described by Regel. Tiling died in 1871 and it seems fairly certain that the visit of Benedict Roezl to America in 1872 was a follow-up of Tiling's brief visit.

Samuel Brannan, Jr., accompanied Dr. Kellogg on his trips botanizing in the Sierra Nevada in 1869 and 1870. Brannan collected insects as well, and the agaristid moth, *Androloma brannani,* was named for him by Stretch.

The year 1869 was a critical one in California history, for it brought the completion of the transcontinental railroad. "Sir: we have the honor to report that the last rail is laid, the last spike is driven. The Pacific Railroad is finished" read the telegram sent from Promontory Point, Utah, to President Grant, on May 10, 1869. It was not long before there set in a growing feeling against the large land holdings under the monopolistic control of the few wealthy men or corporations, such as the very group that had won the railroad triumph. "Out of three drops of rain which fall in the San Joaquin Valley, two are owned by Collis P. Huntington." The big strikes of the early years of the Gold Rush were stories now, the whale oil industry began its steady decline. New industries came with the advent of the railroad. Fruit culture was soon the first agricultural interest of the State. This period of economic transition, like the earthquake of 1868 and its consequences, brought financial restrictions on the Academy.

The newly chartered University of California began classes on September 20 at its old Oakland campus—it was not until 1873 that the move "five miles to the north to the site christened Berkeley" was made—and a man with scientific traditions, John LeConte, served as its third president *pro tem.* His brother, Joseph LeConte, arrived that month to lecture on geology, zoology, and botany; he re-enters our narrative again very soon.

> When I set out on the long excursion that finally led to California I wandered afoot and alone, from Indiana to the Gulf of Mexico, with a plant-press on my back, holding a generally southward course, like the birds when they are going from summer to winter.

So wrote John Muir. After a near-fatal siege of fever in Florida and a short stay in Cuba, Muir arrived in San Francisco by way of the Panama steamer. He soon set out on foot for the Yosemite. *My First Summer in the Sierra* was his diary of 1869. For the next six years Muir—"the wiry young man with auburn hair, full beard, and electric blue eyes had one trait that outweighed all other elements in his nature, the trait of persistence"—absorbed the geology, zoology, and botany of the region and became in turn guide for geologist Joseph LeConte, lepidopterist Henry Edwards, and, in 1872, botanist John Torrey on his second visit to California. Muir wrote "Harry" Edwards under date of June 6, 1872:

> Your bundle of butterfly apparatus is received. You are now in constant remembrance, because every flying flower is branded with your name. I shall be among the high gardens in a month or two and will gather you a good handful of your favorite painted honeysuckers and honeysuckles. I wish you all the deep far-reaching joy you deserve in your dear sunful pursuits.

On February 22, 1873, Muir wrote Asa Gray:

> Our winter is very glorious. January was a block of solid sun-gold, not the thin frosty kind, but of a quality that called forth butterflies and tingled the fern coils and filled the noontide with dreamy hum of insect wings.

Eventually Muir moved down to the big city to write up his Sierra experiences, which appeared first in such journals as the *Overland Monthly.*

> Some of my grandfathers must have been born on a muirland, for there is heather in me, and tinctures of bog juices, that send me to Cassiope, and oozing through all my veins impel me unhaltingly through endless glacier meadows, seemingly the deeper and danker the better.

In the summer of 1870 Joseph LeConte, Professor Frank Soule, Jr., and eight students camped in the Sierras for six weeks. LeConte said, "I never enjoyed anything else so much in my life—perfect health, the merry party of young men, the glorious scenery, and, above all, the magnificent opportunity for studying mountain origin and structure." This summer's foray was the theme of his *Journal of Ramblings through the High Sierras of California by the University Excursion Party,* published in 1875.

The third of the trilogy of mountain essays was Clarence King's *Mountaineering in the Sierra Nevada,* published in 1871. Clarence King, Sheffield Scientific graduate, was twenty years old when, almost providentially, he met Brewer, a Sheffield alumnus, on the steamer plying between Sacramento and San Francisco on August 31, 1863. King was traveling with his college chum James Terry Gardiner, and in a letter to his mother Gardiner described Brewer in these words:

> . . . nothing peculiar about him, yet his face impressed me. . . . the roughest dressed person on the steamboat [with] an old felt hat, a quick eye, a sunburned face with different lines from the other mountaineers, a long weather-beaten neck protruding from a coarse grey flannel shirt and a rough coat, a heavy revolver belt, and long legs, made up the man; and yet he is an intellectual man—I know it.

Three days after meeting Brewer, Clarence King was made an assistant geologist of the State Geological Survey. He lived to climb many of the highest peaks of the Sierra Nevada ahead of others, but King "was an amateur, not a scientific climber, and he delighted in thrills." By his thirtieth birthday he was in charge of the Fortieth Parallel Survey, and soon afterwards he became the first director of the U. S. Geological Survey.

Louis Agassiz visited San Francisco in 1872 en route home from Brazil by way of Cape Horn aboard the *Hassler.* Agassiz visited Joseph LeConte in Oakland on this trip.

During September (or October ?), 1872, Benedict Roezl, native of Bohemia, passed through the city on a plant-collecting foray for European horticultural firms, en route from Panama via Acapulco. The details of Roezl's visit, which must have been brief, as Tiling's was before him, are confused in the few accounts in the literature. The beautiful dull-red flowered gooseberry of middle elevations in the Sierra Nevada, *Ribes roezlii,* was named for him by the botanist Regel.

Gustavus Augustus Eisen, born in Stockholm, Sweden, came to the United States in October, 1872, after taking his Doctor of Philosophy degree at Upsala earlier that year. He apparently headed for California, for he soon settled at Fresno, then a pioneer community. Eisen's most important work was in horticulture. By lectures and pamphleteering he fostered the introduction of the Smyrna fig and avocado into the State. He joined the Academy in 1874 and served as curator from 1892 to 1900. From time to time he collected plants in Fresno County; for example, *Phacelia eisenii,* named by Brandegee. Eisen must be credited, too, for his part in the creation of Sequoia National Park by executive decree. Mount Eisen, elevation 12,000 feet, in the Park, perpetuates his name. Dr. Eisen led Academy expeditions—apparently the first under the Academy's sponsorship—to Lower California in 1892, 1893, and 1894. During those years his interests included helminthology, archaeology, and geology, in addition to botany.

In the 1870's one of the leading taxidermists in San Francisco was Saxon-born

Ferdinand Gruber, the Academy's one-time Curator of Birds. He assisted in the arrangement of the collection of mounted birds at Woodward's Gardens, one of the city's earliest and much-beloved pleasure resorts. The statues and urns that once graced the Gardens may be seen today at Sutro Heights. Gruber invented a rotating tableau of natural history called the "Zoogeographicon," exhibited at the Gardens from 1874 to 1889. Xantus called Gruber "a very excellent taxidermist, and [a man] who sells at a very high figure his birds for drawing room ornaments . . . Mr. Gruber is a very honest man, but a very strict *commerciante* also." It was Gruber who collected birds on the Farallones for Xantus in exchange for skins from Cape San Jose del Cabo, and hereby hangs a tale. Xantus, whose veracity seems to have eroded pretty far on other occasions as well, wished to swell the collection of Cape birds to be sent to Spencer F. Baird at the Smithsonian, so he took Farallon skins of Tufted Puffin and Pigeon guillemot collected by Gruber and attached labels reading "Sandoval point, 1860" and "Cape Los Martires, 1861" to them. These are birds not otherwise known from Lower California and when Joseph Grinnell was preparing his *Distributional Summation of the Ornithology of Lower California* he remarked, without knowing of the switch perpetrated by Xantus or, indeed, of Xantus' exchange contacts with Gruber, that the skins showed a remarkable resemblance to Gruber's well known specimens! There are still unsolved problems of this nature, as witness the hawk *Onychotes gruberi*. It is supposed to have a California origin but is now regarded as a later name for an Hawaiian hawk. Gruber was in touch with Dr. Frick, French Consul General in Honolulu—can this be a clue to the mystery of *Onychotes gruberi?*

Dr. Kellogg found a sympathetic colleague in Dr. Arthur Wellesley Saxe, who came to California in 1850 and worked in the mines until 1852. In 1854 he took up residence as practicing physician at Santa Clara, where he lived until his death in 1891, with one visit to the Hawaiian Islands to study leprosy. Dr. Howard A. Kelly says he was President of the California Horticultural Society and had "one of the largest collections of roses and rare bulbs in the state." Dr. Kellogg named *Rumex saxei* for his friend in 1879, and Professor Greene named *Clarkia saxeana* in 1887, but Saxe's collections at the Academy, which were perhaps never extensive, were lost in the fire of 1906.

A close friend of Harford at the Academy was George Washington Dunn, who came to California in 1850 and worked in the placer mines. Along with many another miner Dunn left the placers penniless, whereupon he determined to devote his life to professional collecting, which seems to have been his first love all along. Taking up residence in San Diego, he ranged far and wide for specimens to sell. He was described as "a genial sort, always on his uppers, who collected insects, plants, shells, and anything else he could sell. Like Micawber, he waited for something to 'turn up'." An acquaintance relates how he would climb a couple of hundred feet up pine trees when he was past eighty, and put lengths of stove pipe on his legs when collecting in rattlesnake-infested areas. He was elected a resident member of the Academy March 16, 1874, and it was at this time that Dunn, along with Harford and some other Academy members, organized the informal Arthrozoic Club. He was admitted into the San Francisco almshouse in his ninety-first year but left of his own accord four months later and died the following year. In all, he made twelve trips to Lower California, including one in 1885 to Guadalupe and Cedros islands with Professor E. L. Greene, and several to Cantillas Canyon, which he was the first naturalist to explore, once with Edward Palmer.

Associated with Harford and Dunn in the Arthrozoic Club was James John Rivers, a broadly trained English biologist and an acquaintance of T. H. Huxley, Charles Darwin, A. R. Wallace, and others. He came to this country in 1867 and arrived in California between 1875 and 1880, having made the friendship of Professor Francis Huntington Snow, of the University of Kansas, in the interim. Rivers was Curator of Organic Natural History at the University of California from 1881 to 1895, when he removed to Santa Monica. His biological interests included insects, shells, spiders, and reptiles, as well as botany.

It was during late February or March in 1874 that the Reverend Edward Lee Greene first came to California from Colorado. An enthusiastic field collector, his coming rather initiated a botanical revival. In Colorado his duties as Episcopalian rector were light and he had filled his days with botany. "But my new parish at Vallejo is too much for me," he wrote Ludwig Kumlein back in Wisconsin. "I have a large congregation and good salary, but with all that, so much pastoral work, that my scientific studies are interfered with not a little." Napa Valley in the spring!—it must have set Greene's botanical senses atingle. Always aware of the importance of the written record against which discoveries must be checked, he repaired to the Academy across the Bay and conferred with Dr. Kellogg. Greene stayed at Vallejo about a year, then returned to Colorado in 1875. He filled the pulpit at Georgetown until March, 1876, then returned to California, this time to Yreka. Along with his shepherding, he found time to botanize on the Humbug Hills that first year and in other directions away from town. On January 21, 1877, he set off for New Mexico and another charge at Silver City, taking his time along the way to collect plants. For the next few years he explored the mountains of western New Mexico and in 1882 returned to California as pastor of St. Mark's Episcopal Church on Bancroft Way in Berkeley. From this time forward Greene took an intense interest in the California flora, and it is agreed that his best work was done with that subject. He spent much of his time at the Academy both while he was at St. Mark's and after becoming the first Professor of Botany at the University of California. It was during this period that he founded the botanical journal *Pittonia*. He continued his field work in California and in Lower California, and from his own and the collections of others described hundreds of new species. The pages of the Academy's *Bulletin* bear witness to his driving capacity for work. The appearance of the *Botany of California* posed a challenge for Greene and some other resident botanists like him to extend the boundaries of our knowledge. Greene's coming to the University as Professor of Botany initiated a program of local exploration into the more remote parts of the State by his students and correspondents. Some of these will be briefly noticed at a later point in our chronicle.

The Centennial Exposition of 1876 called for nation-wide exhibits, including forestry and horticulture, and George Richard Vasey, son of the Washington agrostologist, Dr. George Vasey, came to California for wood exhibits in 1875. He also made general collections of vascular plants as far north as Mendocino County, but his labels have caused some serious confusion from a lack of careful locality data.

The Russian diplomat, Carl Robert Osten Sacken, visited California first in 1875–1876 as a private citizen interested in collecting Diptera. Previous to this he had served as Secretary of the Russian Legation and Consul General of Russia in New York City.

> In many ways he constituted the *beau ideal* of a scientific entomologist: absolute master of numerous languages, independence of means, social rank, retentive memory, accurate observation, possessor of an almost perfect library of works upon Dipterology, and polished manners—these qualities all combined enabled him to hold the highest rank in his special branch of science.

Lyman Belding, "the Nestor of California ornithologists," knew the passenger pigeon in Pennsylvania's Wyoming Valley, and after he came to Stockton in 1854 the elk of the tule marshes and beaver and otter about the valley town were familiar sights to him. In 1862 Belding moved to Marysville, but it was not until the publication of Cooper's *Ornithology of California* in 1876 that his interest took a serious turn. He was no doubt encouraged by S. F. Baird and Robert Ridgway, who guided his collecting energies. They suggested that Belding make a trip to Guadalupe Island in the spring of 1881, but this was abandoned in favor of a visit to Cedros Island. Belding made several trips to Lower California; he made especially notable collections about Cape San Jose del Cabo, where, to his wonderment, Xantus had missed certain common birds. But the high Sierras of central California drew his closest scrutiny, for neither Heermann, Gambel, nor Xantus explored them and Bell may well not have reached much above the foothills. Belding's 274-page account of *Birds of the Pacific District* was published in 1890 by the Academy. He sent several papers to the *West American Scientist* and to *Zoe*.

The lepidopterist, William Greenwood Wright, author of the *Butterflies of the West Coast* (San Francisco, 1905)—a rare book because of the destruction of the warehouse stocks in the fire of 1906—was a well-known figure about the Academy. Henry Edwards, Dr. Behr, R. H. Stretch, and others at the Academy, as well as Dr. Parry, who botanized in Wright's territory about San Bernardino, were all his friends. He was a largely self-educated man, who came to California shortly after the Civil War. For twenty years he operated a planing mill at San Bernardino, devoting his leisure to collecting insects, especially butterflies, and plants. George H. Horn characterized Wright as "a zealous botanist, for whom neither the privations incident to an exploration of the Mojave Desert nor the jealous watchfulness of the Indians, seemed to have held any terrors." In June, 1888, he botanized in the Greenhorn Mountains; in January, 1889, about the Mexican port of San Blas; at Sitka, Alaska, in July, 1891; and in Mendocino County, in May, 1894. His later years were passed at San Bernardino, where he was a familiar figure because of his natural history interests and his fondness for instructing children in the subject, and there he died in 1912, at the age of eighty-three.

Charles Christopher Parry is well known as a botanical explorer of Colorado, and before that as a member of the Mexican Boundary Survey, but he also made several botanical visits to California. Sargent has remarked on the zeal, industry, and intelligence with which he botanized for a period of more than forty-eight years in the West. The winter of 1880–1881 Dr. Parry spent in and around San Francisco, with nominal headquarters at the Academy. Returning in the spring of 1883, he spent that season on excursions both to the north and south of the city. During those years he was able to secure a pass on the Southern Pacific Railroad through the offices of his good friend Dr. Stillman, Leland Stanford's personal physician. He stayed ten months during 1886–1887 investigating the genera *Ceanothus, Arctostaphylos,* and *Alnus.* Though Parry did not write any manuals or even extensive revisions of genera, aside from the synopses of the ceanothi, chorizanthes, and manzanitas, he wrote a fair stream of chatty articles to the local newspapers, as well as to his home-town *Davenport Gazette.* Some of these sketches demonstrate a fine command of English and a poetic quality not often found in such ephemera. He was fond, too, of writing terse messages to his botanical cronies, Englemann, Gray, and to Canby, Redfield, and just about all the contemporary botanical figures of the day, for Parry was friendly and communicative. Typical of these short letters is the following to Samuel Bonsall Parish of San Bernardino, here quoted in part:

> Since leaving your dry region for pastures green, I have been able to see some things that may be of interest to you—at least you deserve an attempt to make them so. Among other things I made a short trip to Ione in Amador Co to look up an anomalous Arctostaphylos collected in leaf only by Mrs Curran last year—I found it on her directions abundant and in full flower Feby 1st of which I secured plenty of specimens—(one of course for you). On subsequent examination I conclude that it is a good n sp— nearly allied to *A. nummularia*—but abundantly distinct. To which I gave the provisional name *A. myrtifolia* n sp. I shall wait to get mature fruit before publishing, and will probably offer it for publication in Cal Acad Bull—when I shall try & tell the whole story.
>
> Another thing that may interest you is an investigation I have been making of our Pacific Coast *Alnus*. . . . So you see there is plenty to be done in studying common things—Greene is busy in his revisions is now at *Boraginaceae* Dr. Gray I hear has commenced printing *Polypetalae.* now in *Papaveraceae.* Will accept most of Greene's *Escholtzias* [sic.]. quite a triumph for Greene. Acad[em]y affairs as you will infer are run *a la Curran* and nobody else has anything to say in the matter—Greene draws off to Berkeley—how long this state of things may last *quien sabe.* I enclose Harkness's inaugural written as I understand by Curran. Let us hear from you. Mrs. P joins in regards to yourself & Mrs. Parish.

Dr. Parry's last visit to California was made in the spring of 1889. For forty years he was a "familiar figure to hunters, prospectors, mountaineers, and all sorts of outdoor people, from the Arizona deserts to the Siskiyou pine forests." Sargent remarked that "no other botanist of his generation . . . revealed so many undescribed North American plants."

During the decade of 1875-1885, with its delays in the publication of the Academy's *Proceedings,* internal dissensions raked the organization. Joseph LeConte said:

> It might be supposed that the Academy of Sciences was an important element in my career [in California] but not so. It had little effect in determining my scientific activity. I read many papers there, to be sure, and several of them were published in their *Proceedings*, but I always reserved the right to publish them elsewhere also.

He remarked further that

> . . . under the presidency of J. D. Whitney the Academy was prosperous and held a high position among the scientific institutions of our country; but from that time, because of internal dissensions, it dropped lower and lower.

The "internal dissensions" of which LeConte speaks were compounded of petty jealousies and institutional politics. Jepson contended that these dissensions were "engineered" by Mrs. Mary K. Curran. Harford served as Director of the Museum from 1876 to 1886, but he "resigned" in altercation. The able Professor George Davidson was replaced as President by Dr. H. W. Harkness. It is clear from Setchell's biography of Mary Katharine Layne Curran Brandegee that he admired her generous qualities and judged her actions disinterested. Professor Jepson, on the contrary, looked upon her activities as scheming and vindictive.

In the professional sense Mrs. Brandegee showed penetrating insight in botanical judgment, as abundantly demonstrated in reviews she prepared for the journal *Zoe*. Though she recorded only the briefest data on her collection labels —as if she intended to stymie another collector revisiting her station!—she made excellent series of specimens illustrating the ecologic variations to be found within a species. She joined the Academy about 1880, after taking her M.D. degree two years before at the University of California, and began studying botany under Dr. Behr. As Mary K. Curran, a widow, without heavy financial obligations, she was able to devote her time and resources to the Academy's Department of Botany fully, and she was made Curator of the Herbarium in 1883. There is no doubt but that she did important spade work for the herbarium, which she described as "in a shocking condition" when she assumed the curatorship. She also became acting Editor of the Academy's *Bulletin*. Katharine Layne's second marriage was felicitous for botany, as for the couple. Marcus Jones remarked to me on one occasion, "Brandegee should have been born a woman and Mrs. Brandegee should have been a man. So their marriage could hardly help being a success!"

Townshend Stith Brandegee came into the Academy's orbit soon after his first visit to California in 1886–1887. It was the winter he came to collect tree trunks for the Jesup collection of woods at the American Museum of Natural History. A student of Daniel Cady Eaton in botany at Yale, where he graduated in engineering, Brandegee went as a young man to Colorado to carry on surveying. He took the opportunity to botanize widely over southern Colorado, as his surveying duties took him to remote districts, and what is more important he had the acumen to recognize the value of his discoveries and to communicate them to Eastern botanists who were in the best position to assist him. Brandegee's self-effacing reticence won him warm friendship from Asa Gray, C. S. Sargent, and others, though his increasing deafness isolated him more and more after he came to live in California. From 1884 to 1890 Mr. Brandegee visited several of the Santa Barbara Islands, one of the most ambitious trips being that to Santa Cruz and Santa Rosa islands in 1888. In 1889 the Academy sent its Curator of Birds, Walter Pierce Bryant, and an assistant, Charles Haines, to Magdalena Bay, and Brandegee joined the party at his own expense, collecting a large series of plants in Lower California that season. It was following this first trip to Lower California that the Brandegees were married, on May 29 in San Diego, after which they set out on foot overland to San Francisco on a botanical honeymoon! For five years thereafter the Brandegees made their headquarters at the Academy, until 1894 when they moved to San Diego. A modest and unassuming man, Brandegee expressed himself crisply on occasion. On one of the several trips to San Jose del Cabo, when he attended the church there more out of deference to the prevailing *mores* than to his own beliefs, he quipped: "Religion sits very lightly on the males—they think it good for women and children."

The notable event of 1877 was the visit of the botanists Hooker and Gray to California. Traveling together they both recorded their impressions and from their letters, fortunately rather fully published, we can gain some first-hand knowledge of California in that era. In San Francisco they stopped at the Palace Hotel, went to Mount Shasta with a pause at Chico: "the trip to Shasta involved long stagecoach journeys, but they were most interesting. Returning to Sacramento we went on to Truckee, where Lemmon joined us by appointment. We gave one day to Mount Stanford and one to Tahoe, then took the overland train as it came on at midnight." Hooker was alarmed at the destruction of the sequoias in the Calaveras grove which they visited: "the doom of these noble groves is sealed." Hooker also decried the wasteful lumbering practices that he saw. After the trip, Gray put it succinctly when he wrote: "we should like to do it all over, and more."

> There is no set of chaps so unblushing as naturalists; they are always wanting something that the other party don't care a straw about.

Thus wrote Alexander Agassiz, from Cambridge, Mass., April 9, 1879, to William Sillern. Agassiz continues:

> Nevertheless, I am going to ask you to put yourself out for me and get me one of the large Cuttle Fish which used to be so common in San Francisco market when I was there. The room in the Museum [of Comparative Zoology at Cambridge] devoted to the beast and its nearest allies is nearly ready, and I am greatly in want of a large Cuttle Fish to scare small boys and frighten women. I don't want him too big, say not more than five feet when fully expanded. The Chinamen used to get them very often, of all sizes, in their nets and then cut them up and sell them to unsuspecting Frenchmen who mistook the species for frogs' legs. Now if Ralston[4] has left any Chinamen in San Francisco, can you speak to a promising specimen of Mongolian and ask him to cling to a good specimen, if the species does not freeze to him. Then by a judicious cutting open of his lower side, so as to let alcohol into his insides, put him into a keg of alcohol and ship him, via Panama, to your humble servant, who will receive him with open arms.

The next time you visit the Blaschka glass flowers at Cambridge remember Agassiz' cuttle fish in the next room!

A zoologist who was to figure prominently in the Academy's history later on was Barton Warren Evermann, whose first California appointment was as superintendent of public schools at Santa Paula, in Ventura County, from 1879–1881. He was interested in birds and plants at that time, especially birds. On his twenty-second birthday, October 24, 1875, Barton Evermann married Meadie Hawkins and she assisted him in preparing bird skins, and in collecting plants. They assembled a good library but this was lost by fire in 1889 at Indiana State Normal School. After his return to Indiana State University for advanced studies, Evermann came under the lasting influence of David Starr Jordan, to weld a friendship that was to yield rich rewards in scientific authorship. He was special lecturer at Stanford in 1893–1894, and in the years between 1896 and 1902,

4. William C. Ralston of Bank of California fame. The thousands of Chinese employed in the construction of the transcontinental railroad flocked to San Francisco and by 1872 they constituted about half the factory workers in the city. The Chinese Exclusion Act of 1880 was the result of the campaign to rid the state of Chinese cheap labor.

alone or in collaboration with Jordan, he published works of classic importance on North American fishes. Evermann published in all 387 books and articles, of which about half are devoted to fishes.

It was natural that exploration of Alaska often involved San Francisco, for the scientific corps commonly assembled there before departure. Charles Haskins Townsend acted as naturalist on the Revenue Steamer *Corwin* in 1885, and on the U. S. Fish Commission Steamer *Albatross* in 1886–1896. Townsend first came to California in 1884 as a field naturalist to collect zoological specimens for the U. S. National Museum. But the *Albatross* expedition was the most important trip for on it he collected some plants, along with mostly vertebrate material along the Alaskan coast. In other years he visited the Marquesas, Paumotu, Society, Cook, Tonga, and Fiji archipelagoes. Then for thirty-five years he served as Director of the New York Aquarium, and his conservation efforts to save from extinction the Alaskan reindeer, Pribiloff fur seal, and Galapagos tortoise earned for him the true gratitude of thoughtful citizens everywhere.

We have remarked on the part that Professor Greene played in stimulating botanical exploration among his students at Berkeley. One of them, Frederick Theodore Bioletti, tells it this way:

> We belonged perhaps to the romantic school of botany. We used the field of botany not as a laboratory but as a playground. Our heroes were not De Bary, nor Strasburger nor Zimmerman, not even Prantl and Engler, but Theophrastus, Rafinesque, and Edward Lee Greene.

Bioletti came to be best known as a viticulturist and professor of that subject at his alma mater. In Professor Greene's class with Bioletti were W. L. Jepson, Victor King Chesnut, Walter Blasdale, and Bioletti's particular chum and companion on field trips, Charles A. Michener. Of one of these Bioletti writes:

> Victor Chesnut we looked upon as an enemy and outlaw. He had collected a *Ribes* and a *Trifolium* in the Napa-Sonoma Mountains in the heart of our main hunting grounds. If we had known his territory we would have invaded it without scruple. To capture a beautiful and apparently new *Ribes* in a remote gorge on the slopes of Hood's Peak, to bring it back to camp in triumph and then to find that it had already been branded *Ribes victoris* was intolerable.
>
> Professor Greene as the Great Chief was of course free from all restrictions. We had too much to gain from his friendship to object to his hunting on our grounds. It was Professor Greene who used the names Michener and Bioletti several times in christening some of our discoveries. For this we were deeply grateful.

Chesnut entered the United States Department of Agriculture in 1894 in charge of poisonous-plant investigations, his previous instruction in chemistry at Berkeley serving him well as a background. His *Principal Poisonous Plants of the U. S.* was one of the most popular publications ever issued by the Government, widely copied in the press of the day and translated into French, German, and Bohemian. Elmer Reginald Drew, with whom Chesnut often botanized in the north Coast Ranges, became Professor of Physics at Stanford. Edwin C. Van Dyke, M.D., Assistant Professor of Entomology at Berkeley, was another student of Professor Greene's, and the botanist, Ivar Tidestrom, one of his last before he left Berkeley for Washington.

Greene himself botanized on San Miguel Island during the summer of 1886, leaving Santa Barbara August 19 and landing at Cuylers Harbor nine days later. The island had been visited by Cabrillo in the winter of 1542–1543, and his exhausted body had been lowered into an unmarked grave. Greene did not find the treasure chest perennially sought by the Conquistadores but he did discover some remarkable endemic plants on the island. In 1887 Joseph LeConte published in the Academy's *Bulletin* a paper entitled "The Flora of the Coast Islands of California in Relation to Recent Changes of Physical Geography" from the data supplied by Professor Greene, "though the interpretation of [the data] was entirely my own," says LeConte.

In addition to Greene's students there was an array of country school teachers and ranchers, wives of miners, and travelers, who corresponded with the Berkeley professor and sent him notable collections. C. C. Marshall was a teacher who collected around Eureka in the mid-1880's. J. B. Hickman taught school at Carneros, in Carneros Canyon, on the Natividad road in the San Miguel Hills and spent his Saturdays and vacations searching the countryside for new plants. Andrea Massena Norton was born at Lanesboro, Susquehanna County, Pennsylvania, September 7, 1853, and taught school for twelve years at Gonzales, Monterey County, beginning in 1880. He was for part of that period also a member of the County Board of Education. It was J. B. Hickman, a fellow teacher and close friend, who introduced Andrea Norton to the *scientia amabilis.* The very restricted *Eriogonum* of the Pinnacles region, and the Monterey County *Chorizanthe* that bear his name were but two of his botanical discoveries.

Some day a historian will tell the story of California's natural history from the vantage point of the ranches where the naturalists foregathered as field bases. There will be Talley's ranch in San Diego County, and Warner's ranch; the Parish ranch near San Bernardino; Duffield's ranch in the Sierra foothills; and the Ricksecker farm in Sonoma County, to mention a few. Lucius Edgar Ricksecker was an entomological collector and a propagator of insects for specialists and cabinet collectors. When not employed as surveyor for Sonoma County, he lived on his farm at Sylvania near the present site of Camp Meeker. He came to California in 1873 after serving as a corporal in the Civil War and maintaining a short residence in Salt Lake City. The insects associated with the sand dunes of Marin County and about San Francisco interested Ricksecker, and he found that his talents for netting unusual forms was profitable. Except for a short residence at Spokane, he lived continuously in the State from 1873 until his death in 1913. To his farm at Sylvania came many Academy members, including Harkness, to search for truffles and other fleshy fungi; Harford, for spiders; Rivers, for Lepidoptera and Coleoptera; and Mary Katharine Curran, for plants.

William C. Bartlett of the *San Francisco Bulletin* remarked in an article published in the *Overland Monthly* for December, 1875, that "through the munificence of a single citizen, the Academy of Sciences has been handsomely endowed, and will soon be equipped for effective work." The benefactor will be recognized as James Lick, who gave the property for the erection of the new museum building for the Academy on Market Street, between Fourth and Fifth streets. This new center of activity, with its fine display features for museum exhibits, was the parent of the California Botanical Club, founded on March 7, 1891, "in response to a call" from seven Academy members—something still miraculous about that number seven!—Harkness, Behr, Eisen, the Brandegees, Townshend and Kate, Mrs. Mary W. Kincaid, and Miss Agnes M. Manning, to bring the Pacific Coast botanists closer together. Ninety-nine signatures appeared on the charter roll, from Carl Purdy on the north to Cleveland, Parish, and Hasse, from southern California, to mention only a few well known figures. C. F. Sonne, G. P. Rixford, (Mary) Elizabeth Parsons, and Alice Eastwood were among the charter members resident in San Francisco. Miss Eastwood was leader of the Club after Mrs. Brandegee moved to San Diego, the meetings being held nearly every week "to study living plants, both native and exotic." From this more or less informal study group have come valuable collections for the Academy's herbarium. In this connection the collections of Evelina Cannon, Caroline L. Hunt, Mary C. Bowman, Mrs. E. C. Sutliffe, Ella Dales Cantelow, and others across the years, are notable.

In the fall of 1895 David Starr Jordan was elected President of the Academy and in his autobiography, *Days of a Man,* he inventories his impressions:

> This useful institution struggled on for years with inadequate support until endowed by James Lick in 1876. Its funds were then mainly invested in a large office building in San Francisco, the museum occupying cramped quarters at the rear. For some time previous to my election [Jordan continues] the Academy membership had been divided into two warring factions—one led by Dr. Davidson, the other by Dr. Harkness, a physician of prominence and an expert in the study of fungi, especially of the group known as truffles. Both men were vigorous and rather intolerant, a combination of qualities which was not rare in pioneer days, and disrupted more than one California organization even as it affected the famous "society on the Stanislow." Indeed, it is reputed that the discords in the institution furnished the motive for Bret Harte's satirical verse.[5]

Harkness expressed a desire to retire in Jordan's favor, and Jordan says, "I then endeavored, with fair success, to put an end to the old feud." Between 1898 and 1911, during Jordan's intermittent presidency, he remarks:

> [The] Academy publications were raised to a very high standard as to number, scientific value, and typographical appearance. For this, special credit was due Dr. Ritter, the editor; and it should be added that the same level of excellence has been continuously maintained by our successors.

During these years the Academy's library and collections were growing steadily. To select one of many areas of activity for illustration, we note that the botanical department acquired the George Thurber herbarium, rich in the Government Railroad Survey collections, and a good set of those of the Death Valley Expedition. Fifty years after the Academy's founding, Professor T. D. A. Cockerell wrote in the *Popular Science Monthly* for April, 1903:

> The civilization of the West is so young that perhaps we ought not to expect much of the native-born therein . . . indeed a very good crop of young men and women, who will be prominent in the next twenty years. Everything shows that California, in particular, will be the center of great biological activity.

Cockerell's prophecy was amply borne out, though interjected in those years was the destruction of the most valuable collection center in the West by the fire of 1906 when "a single day saw the destruction of a museum and a library that had been fifty years in building. Of thousands of books and specimens of almost priceless value, nothing was saved except what could be loaded into one spring wagon and carted to safety ahead of the fire." As Dr. Robert C. Miller, present Director of the Academy, continues:

5. The "warring factions" of the 1890's postdated the publication of Bret Harte's verse, which perhaps rests on the altercations of the 1860s.

That anything at all was saved was due especially to Miss Eastwood, then as now [1942] the Academy's curator of botany, who lost all of her own possessions while attempting to save those of the Academy. . . . It was justice in the most poetic sense that more than half a century after the Academy had voted to admit women to its activities, the book of minutes containing the record of that action, along with other documents and specimens of inestimable value, should have been saved through the energy and resourcefulness of a woman curator.

Alice Eastwood first visited California in 1890 as a tourist, then returned the next year for a brief but active visit engaged in Academy affairs. In 1892 she joined the Academy staff as joint Curator of Botany with Mrs. Katharine Brandegee. Following Mrs. Brandegee's taking up residence in San Diego in 1894, Miss Eastwood became the Academy's Curator and head of the Department of Botany. She struck her characteristic stride in a series of papers published in the *Botanical Gazette*, the *Bulletin of the Torrey Botanical Club*, and the *Proceedings* of the Academy on the California flora. She prefaced *A Handbook of the Trees of California* with the statement that "the pressing need of a popular manual of the trees of California is the reason for this little book." "Throughout the work the aim has always been brevity and clearness—the desire to help rather than to shine." Endowed with unusual energy, she rebuilt the Academy's botanical resources and initiated many worth-while activities. These ranged from the around-the-year "live exhibit" of named flowering specimens in the Academy's foyer for the instruction of visitors to the republication of Lindley's useful glossary of botanical terms and the initiation of the *Leaflets of Western Botany*, a periodical founded jointly with John Thomas Howell, the present Curator of Botany. For Alice Eastwood, as for Sir Christopher Wren, we may well recall his motto, *Si monumentum requiris, circumspice.*

The Academy's first salaried director was B. W. Evermann, whose California residence from 1879 to 1881 as a school superintendent has been mentioned. Beginning in 1914 Dr. Evermann served the Academy for eighteen years. In 1915 he reported 20,000 specimens in the Department of Birds; 31,500 reptiles and amphibians, including 266 specimens of the Galapagos land tortoises; and the recent acquisition of the Hemphill conchological collection of over 60,000 specimens. At that time Evermann reported that the Academy's herbarium contained more than 18,000 sheets. The collections were then temporarily housed at 343 Sansome Street, but soon were installed at the new quarters in Golden Gate Park. Under Dr. Evermann's direction the Academy grew in prestige and importance. A hard-driving worker for himself as for others, he introduced the punching of time clocks on one occasion! Evermann made capital gains during his years at the Academy. In addition to his own research studies on fishes and the bringing of the Eigenmann South American fish collections to the Academy as the nucleus of its ichthyological department, he implemented the Steinhart Aquarium in 1921 and eight years later the Leslie Simson habitat groups of African wild life. During his directorship the Academy published twenty-five volumes of scientific reports. His energies were so thoroughly dedicated to the Academy and the natural sciences that it is doubtful if he gave more than passing thought to the amenities of social living. Certainly the awesome severity he evinced toward his Academy associates was more defensive than real.

During Evermann's directorship John Van Denburgh served as Curator of Reptiles and his assistant was the present curator, Joseph R. Slevin, most widely known for his detailed knowledge of Galapagos reptiles, who will have completed fifty years of service to the Academy in 1954. Leverett Mills Loomis, who served as director before Dr. Evermann, was later curator of sea birds. Though a competent ornithologist, Loomis' stern, uncompromising opinions ruffled other feathers from time to time. There was no question, however, but that Loomis was an able "museum man."

In entomology the Academy's collections and reputation grew under the curatorship of a coleopterist, E. C. Van Dyke, who served from 1904 until 1916, assisted by Carl Fuchs. Later E. P. Van Duzee, a hemipterist, became curator of the collections and edited the *Pan-Pacific Entomologist,* a periodical aided financially by the Academy.

"History itself," writes Professor Frederick J. Teggart, "does not seek to elucidate the future; it takes account only of the steps by which the present situation has come to be as it is." Prophecy, then, has no proper place in this sketch. The emphasis has been rather on the character of the naturalist, his sources and resources, his efforts to found an Academy of Sciences devoted first to the descriptive fields of the natural sciences and more recently metamorphosing into an interpretative effort where the accumulated facts may be fitted into a possible pattern.

Dr. Stillman, the pioneer naturalist-physician of San Francisco, wrote a bit wryly:

> Of those who returned to their old homes [from California] to enjoy the fruits of their enterprise we know but little, we pity them much. . . . To them and our children we leave this beloved land. . . . We have not all realized the hopes that made radiant the morning of our lives and sustained us through so great hardships;—fortune was ever a capricious goddess. . . . Our brethren told us [in 1849] to go in freedom's name and possess the land—"to read no more history until you have made it."

Crescit scientia!

Roster of Biographies

This roster is planned as a guide to biographical references to persons, both visitors and residents, who have become associated with San Francisco, a contribution toward some ultimate "Meisel" for California natural history. "San Francisco" as used in the title is inclusive and refers to the general San Francisco Bay region but does not extend south of the Stanford habitat nor north of Marin County. "Naturalist" herein accents the natural history collector but includes resident persons who have been traditionally associated with such collections as descriptive biologists. The time limits extend from the earliest contacts subsequent to the purely historic figures whose role was merely incidental (and are thus not included) to the present time, but no effort has been made to include all the contemporaries since to do so would amount to reproducing membership lists of local organizations and to throwing the whole portrait of the growth of San Francisco natural history out of focus.

The plan of this roster follows certain other bibliographic tools of this nature, provided by Britten and Boulger in England, by Ignatz Urban for the West Indies, and by the author for the Rocky Mountain region. Code words in italics used to abbreviate sources wherein biographical materials may be found are explained in the introductory list of abbreviations. Ancillary references to the usual sources are given; indeed, many of the better known references are omitted for the more prominent persons in the interest of saving space in favor of overlooked commentary. Particular effort has been made to list less familiar sources of information. These sometimes include commentary of a very incidental nature in autobiographies and the like where persons may be succinctly evaluated as well as identified.

A few important general accounts of reference value to anyone concerned with the San Francisco region are indicated by an asterisk prefixed to the code word in the following list.

ABBREVIATIONS

The following biographical directories, dictionaries, and various published sources of information on the life, travels, and collections of naturalists associated with San Francisco are referred to by the italicized abbreviation explained here:

ACAB Appleton's Cyclopedia of American Biography, ed. by J. G. Wilson and John Fiske with rev. supp. New York, 1887–1924.

**Alden* Alden, Roland H., and John D. Ifft, Early naturalists in the Far West. Occ. Pap. Calif. Acad. Sci., 20:i–v, 1–59. 1943.

ADB Allgemeine Deutsche Biographie. Leipzig, 1875–1912.

Amsci American Men of Science, ed. by Jacques and J. McKeen Cattell. Ed. 1 (1906); ed. 2 (1910); ed. 3 (1921); ed. 4 (1927); ed. 5 (1933); ed. 6 (1938); ed. 7 (1944).

Badè Badè, William Frederic, Life and Letters of John Muir. Boston and New York, 1923–1924.

Blankinship Blankinship, Joseph William, A century of botanical exploration in Montana, 1805–1905: collectors, herbaria and bibliography. Montana Ag. Coll. Sci. Studies Bot., 1:1–31. 1904.

Bradley Bib. Rehder, Alfred, Bradley Bibilography. A Guide to the Literature of the Woody Plants of the World Published Before the Beginning of the Twentieth Century. 5 Vols. Cambridge, Mass., 1911–1918.

**Brewer* Brewer, William H., List of persons who have made botanical collections in California. In Sereno Watson, Botany of California, 2:553–559. 1880.

Brewster Brewster, E. T., Life and Letters of Josiah Dwight Whitney. Boston, 1909.

Britten Britten, James, and George S. Boulger, A Biographical Index of Deceased British and Irish Botanists. Ed. 2. London, 1931.

Butler Butler, Ruth Lapham, A Check List of Manuscripts in the Edward E. Ayer Collection. Newberry Library, Chicago, 1937.

Candolle de Candolle, Alphonse, La Phytographie. Paris, 1880, esp. pp. 383–462.

Carpenter Carpenter, Mathilde M., Bibliography of biographies of entomologists. Amer. Midl. Nat., 33:1–116. 1945.

DAB Dictionary of American Biography. ed. by Allen Johnson and Dumas Malone. New York, 1928–1937, and Suppl. I, 1944.

Dall Dall, William Healey, Spencer Fullerton Baird, a Biography. Philadelphia and London, 1915.

DNB Dictionary of National Biography. ed. by L. Stephen and S. Lee. London. 1885–1901, and supplements.

Dean Dean, Bashford, A Bibliography of Fishes. 3 vols. Amer. Mus. Nat. Hist.. New York, 1916–1923.

**Eastwood* Eastwood, Alice, Early botanical explorers on the Pacific Coast and the trees they found there. Calif. Hist. Soc. Quart. 18(4):335–346. 1939.

Embacher Embacher, Friedrich, Lexikon der Reisen und Entdeckungen. Leipzig, 1882.

**Essig* Essig, Edward Oliver, A History of Entomology. New York, 1931.

Ewan Ewan, Joseph, Rocky Mountain Naturalists. Denver, 1950.

Farquhar's Brewer Farquhar, Francis P., ed., Up and Down California, the Journal of William H. Brewer. New Haven, 1930. Reissued, Berkeley, Univ. Calif. Press, 1949.

Farquhar's Yosemite Farquhar, Francis P., Yosemite, the Big Trees and the High Sierra, a Selective Bibliography. Berkeley and Los Angeles, 1948.

Geiser-two Geiser, Samuel Wood, Naturalists of the Frontier. Ed. 2. Dallas, 1948.

Gray Gray, Jane Loring, Letters of Asa Gray, 2 vols. Boston, 1893.

Harshberger Harshberger, John William, Botanists of Philadelphia and Their Work. Philadelphia, 1899.

Howell Howell, John Thomas, Marin Flora. Berkeley and Los Angeles, 1949.

Hughes Hughes, Katherine Whipple, A Contribution Toward a Bibliography of Oregon Botany with Notes on the Botanical Explorers of the State. Oregon State College Thesis Ser. no. 14 (mimeographed). 1940.

Hultén Hultén, Oskar Eric Gunnar, History of botanical exploration in Alaska and Yukon territories from the time of their discovery to 1940. Bot. Not., 1940: 289–346. Map. 1940.

Hume Hume, Edgar Erskine, Ornithologists of the United States Army Medical Corps. Baltimore, 1942.

Huxley's Hooker Huxley, Leonard, Life and Letters of Sir J. D. Hooker. 2 vols. London, 1918.

**Jepson* Jepson, Willis Linn, Botanical explorers of California—I, Madroño 1:67–170 (1928).—II, 1:175–177 (1928).—III, 1:183–185 (1928).—IV, 1:188–190 (1928).—V, 1:214–216 (1929).—VI, 1:262–270 (1929).—VII, 2:25–29 (1931).—VIII, 2:83–88 (1933).—IX, 2:115–118 (1934).—X, 2:130–133 (1934).—XI, 2:156–157 (1934).

Kelly Kelly, Howard A., Some American Medical Botanists, Commemorated in Our Botanical Nomenclature. Troy, N. Y., 1914.

Lasègue Lasègue, A. Musée Botanique de M. B. Delessert. Paris, 1845.

Lemmon Lemmon, John Gill, Oaks of the Pacific Slope, pp. 1–19. 1902. Reprinted from Trans. Pac. States Floral Congress, Oakland, 1902. Copy examined in the Ref. Lib. of Univ. Calif. Herb., Berkeley.

Liverpool Stansfield, H., ed., Handbook and Guide to the Herbarium Collections in the Public Museums, Liverpool, 81 pp. 1935.

**Meisel* Meisel, Max, Bibliography of American Natural History, 3 vols. New York, 1924–1929.

Moldenke Moldenke, Harold N. and Alma L., A brief historical survey of the Verbenaceae and related families, Pt. II (Biographical). Plant Life (H. P. Traub, ed.), 2:46–98. "1946," 1948.

Musgrave Musgrave, Anthony, Bibliography of Australian Entomology, 1775–1930, with Biographical Notes on Authors and Collectors. Sydney, 1932.

NBG Hoefer, J. Ch. F., Nouvelle Biographie Universelle (later, Générale). Paris, 1852–1866.

NCAB National Cyclopedia of American Biography, ed. by "distinguished biographers," Ainsworth R. Spofford, advisory ed. New York, 1898–1947. Current vols. 1930–1948.

Osborn Osborn, Herbert, Fragments of Entomological History. Including Some Personal Recollections of Men and Events. Pts. I and II. Columbus, Ohio, 1937–1946.

**Palmer* Palmer, Theodore Sherman, Notes on persons whose names appear in the nomenclature of California birds. A contribution to the history of West Coast ornithology. Condor, 30:261–307. 1928.

Pennell Pennell, Francis Whittier, Botanical collectors of the Philadelphia local area. Bartonia, 21:38–57, 1942; 22:10–31, 66. 1943.

Piper Piper, Charles Vancouver, Flora of Washington, Contr. U. S. Nat. Herb. 11:10-20. 1906.

Rodgers' Gray Rodgers, Andrew Denny, III, American Botany, 1873–1892, Decades of Transition. Princeton, 1944.

Rodgers' Torrey Rodgers, A. D., III, John Torrey, a Story of North American Botany. Princeton, 1942.

Rydberg Rydberg, Per Axel, Scandinavians who have contributed to the knowledge of the flora of North America. Augustana [College, Rock Island, Ill.] Library Publ. no. 6, pp. 5–49. 1907.

Sargent Sargent, Charles Sprague, Silva of North America. 14 vols. Boston, 1891–1902.

Sherborn Sherborn, Charles Davies, Where is the —— Collection? An Account of the Various Natural History Collections Which Have Come Under the Notice of the Compiler. Cambridge Univ. Press, 1940.

**Stillman* Stillman, J. D. B., Seeking the Golden Fleece; a Record of Pioneer Life in California . . . , esp. pp. 285–326. San Francisco, 1877.

**Stone* Stone, Witmer, Philadelphia to the coast in early days, and the development, of western ornithology prior to 1850. Condor, 18:3–14, 1916.

Swainson Swainson, William, Taxidermy, with the Biography of Zoologists, and Notices of their Work. London, 1840.

Urban Symb. Ant. Urban, Ignatz, in Symbolae Antillanae. 3:1–158. Berlin, 1898.

Urban Fl. Bras. Urban, Ignatz, Flora brasiliensis. Vol. 1, pt. 1. 1906.

Van Steenis Van Steenis-Kruseman, M. J., Flora Malesiana, 1:i–clii, 1–639. 1950.

Wagner-three Wagner, Henry R., The Plains and the Rockies. Ed. 3, by Charles L. Camp. Columbus, Ohio, 1953.

Woodcock & Stearn Woodcock, H. B. D., and William T. Stearn, Lilies of the World. London and New York, 1950.

BIBLIOGRAPHY

Adams, James Capen

J. Grinnell, J. S. Dixon, and J. M. Linsdale, Fur-bearing Mammals of California, 1:78–80, 1937.

Agassiz, Alexander Emmanuel Rudolphe, 1835–1910

Carpenter, 2; *DAB; Meisel*, 1:156; A. G. Mayer in Pop. Sci. Mo., 77: 418–446 (portr.), 1910; G. R. Agassiz, Letters and Recollections of Alexander Agassiz, 161–162 *et passim*. 1913; G. L. Goodale in Nat. Acad. Sci. Biog. Mem., 7:291–305 (portr.), 1912.

Agassiz, Jean Louis Rudolphe, 1807–1873

Carpenter, 2; *DAB; Dall*, *passim; Meisel*, 1:157–158; *Sherborn;* D. S. Jordan in Science, n.s., 16:250, 1902, and Days of a Man, 1:107–117 (portr.), 1922; W. J. Youmans, Pioneers of Science in America, 475–491 (portr.), 1896.

Allen, Charles Andrew, 1841–(?)

Badè, 2:71, but perhaps not this person (?); *Palmer*, 264; cf. Forest and Stream 7:4, Aug. 10, 1876.

Ames, Mary E. Pulsifer, 1845–1902

Brewer, 558; Boston Evening Transcript for Mar. 21, 1902.

ANDERSON, CHARLES LEWIS, 1827–1910

Brewer, 558; *Jepson*, 1:214–216 (portr.), 1929; *Wagner-three*, 219a.

ANDERSSON, NILS JOHAN, 1821–1880.

Brewer, 557; *Rydberg*, 25; *Urban Fl. Bras.*, 1:1; *Van Steenis* 16.

ANDREWS, TIMOTHY LANGDON, 1819–1908

Brewer, 557; *Howell*, 30; L. M. Pammel in Cedar Rapids [Iowa] Daily Republican for Mar. 19, 1908 (portr.).

AUDUBON, JOHN WOODHOUSE, 1812–1862

Dall, 155 *et passim; Geiser-two*, 270; *Meisel*, 1:161; *Wagner-three*, 176, 208; H. Harris in Condor, 43:34, 1941; Maria R. Audubon, Audubon and His Journals, ed. by E. Coues, *passim*, 1898.

AUSTIN, REBECCA MERRITT SMITH LEONARD, 1832–1919

Brewer, 558; *Jepson*, 2:130–133 (portr.), 157; M. A. H[ail] [daughter of Mrs. Austin] in Plumas [County] National Bulletin, vol. 53 no. 29, for Mar. 27, 1919, copy examined in Frank Morton Jones Library, Wilmington, Del.; H. S. Reed in Oakland [Calif.] Tribune for Dec. 28, 1941; F. M. Jones in Delaware Notes, ser. 23:24–35, 1950.

AYRES, WILLIAM ORVILLE, 1817–1891

Dean, 1:45; *Dall*, 154; *Farquhar's Yosemite*, 11, 26, etc., for Thomas A. Ayres, whose relationship to Wm. O. Ayres is undetermined; cf. A. Kellogg in Proc. Calif. Acad. Sci. for Feb. 3, 1873, for proposed genus *Ayresia*.

BAKER, MILO SAMUEL, 1868–

Ewan, 155; cf. Madroño, 4:283, 1938.

BARCLAY, GEORGE

Brewer, 555; *Britten*, 19; cf. *Palmer*, 268 *s.v.* Belcher; *Van Steenis*, 36.

BARKELEW, FREDERICK E.

Cf. E. W. Nelson in Mem. Nat. Acad. Sci., 16:144, 1921; I. M. Johnston in Proc. Calif. Acad. Sci., ser. 4, 20:13, 1931; P. A. Munz in Leafl. West. Bot., 7:73, 1953.

BARLOW, CHESTER, 1874–1902

Palmer, 267; W H. Osgood in Auk, 20:92–93, 1903; H. R. Taylor in Condor, 5:3–7 (portr.), 1903.

BEARDSLEY, A. F.

Brewer, 557; *Farquhar's Brewer*, 218–219; R. C. Miller in Calif. Hist. Soc. Quart., 21:366, 1942, as "A. F. Beardslee," quoted from Academy's *Proc.*

BECK, ROLLO HOWARD, 1870–

Palmer, 267–268; R. C. Murphy, Oceanic Birds of South America, 2:25 (portr., pl. 1), 1936.

BEECHEY, FREDERICK WILLIAM, 1796–1856

Britten; DNB; Stillman, 319–325.

BEHR, HANS HERMANN, 1818–1904

Brewer, 556; *Britten*, 339; *Carpenter*, 7; *Essig*, 553–556 (portr.); cf. *Geiser-two*. 271; *Meisel*, 1:164; anon. in Entom. News, 15:142–144, 1904 (from San Francisco Chronicle); A. Eastwood in Science, n.s., 19:636, 1904; autobiog. notes in Erythea, 4:168–173, 1896; A. E. Zucker, Forty-eighters, 277, 1950.

BELCHER, EDWARD, 1799–1877

Britten; DNB; Stillman, 325.

BELDING, LYMAN, 1829–1917

Palmer, 268; autobiog. notes in Condor, 2:1–5, 1900; A. K. Fisher in Auk, 37:33–45 (portr.), 1920; W. K. Fisher in Condor, 20:51–61 (portr.), 1918.

BELL, JOHN GRAHAM, 1812–1889

Dall, 89–91; *Palmer*, 268; *Stone*, 12–13; "Scientific Arena" for Aug., 1887; F. M. C(hapman) in Auk, 7:98–99, 1890; J. F. McDermott, Up the Missouri with Audubon, *passim*, 1951.

BIDWELL, ANNIE E. KENNEDY (MRS. JOHN BIDWELL)

Badè, 2:72 *et passim;* R. D. Hunt, John Bidwell, Prince of California Pioneers, Caxton Press, Caldwell, Idaho, 1942; D. S. Jordan, Days of a Man, 1:471, 1922.

BIGELOW, JOHN MILTON, 1804–1878

Brewer, 557; *Ewan*, 164; *Geiser-two*, 271; *Meisel*, 1:165, 3:194, etc.; *Howell*, 30; *Sargent*, 1:88; *Wagner-three*, 265; A. E. Waller in Ohio Arch. and Hist. Quart., 51:313–331, 1942.

BIOLETTI, FREDERICK THEODORE, 1865–1939

Bradley Bib., 1:320; *Howell*, 31; autobiog. in Sci. Mo., 29:333–339, 1929; obit. in Science, 90:364, 1939.

BLACK, GEORGE, fl. 1850–1855

Brewer, 557. An associate of William Lobb; a San Franciscan?

BLAISDELL, FRANK ELLSWORTH, 1862–1946

Amsci, ed. 7; *Hultén*, 316; cf. A. Eastwood in Bot. Gaz., 33:126–149, 199–213; 284–291, 1902.

BLAKE, JAMES

Meisel, 3:539; C. D. Leake in Calif. Monthly, 38:22 *et seq.*, 1937.

BLAKE, WILLIAM PHIPPS, 1825–1910

DAB; Farquhar's Brewer, passim; Geiser-two, 271, where dates given as "1828–1910"; *NCAB*, 25:202–203, as 1826–1910"; R. W. Raymond in Amer. Inst. Mining Engineer. Trans., 4:851–864, 1910.

BLASCHKE, EDUARD LEONTJEVITCH

Bradley Bib., 1:453; *Essig*, 557–558; *Hultén*, 300.

BLASDALE, WALTER CHARLES, 1871–

Amsci.

BLOOMER, HIRAM G., 1821–1874

Brewer, 557; W. L. Jepson in Erythea, 7:163–166 (portr.), 1899; *Woodcock & Stearn*, 232.

BOLANDER, HENRY NICHOLAS, 1831–1897

Brewer, 558; *Candolle*, 397; *Howell*, 31; *Woodcock & Stearn*, 160, as "Henry Nicholson Bolander"; W. L. Jepson in Erythea, 6:100–107 (portr.), 1898; "Directions for bot. collecting" in Calif. Teacher, 1:131–132, Dec., 1863; C. Purdy in Madroño, 2:33–34, 1931.

BOTTA, PAOLO EMILIO, 1802–1870

Alden, 31–32; *Brewer*, 555; *Embacher*, 44–45; *Palmer*, 269; *Stone*, 7; *NBG;* T. S. Palmer in Condor, 19:159–161, 1917; J. Grinnell in Univ. Calif. Publ. Zool., 38:275 *et passim*, 1932.

BOUCARD, ADOLPHE, 1839–1905

Sherborn, 21; ed. note in Nature, 4:50, May, 1871; T. S. Palmer in Condor, 19:168, 1917; C. A. Kofoid in Condor, 25:85–89, 1923; W. F. H. Rosenberg in Condor, 26:38–39, 1924; J. Grinnell in Pac. Coast Avifauna, 16:12, 1924, for description of Boucard's

"Travels of a Naturalist," 1894, comprising a series of collected chapters first published in The Humming Bird [London], Vol. 3, Mar. 1893, to Vol. 4, Dec. 1894. Boucard landed in San Francisco Aug. 15, 1851, and remained a year, collecting birds and insects.

BRACKENRIDGE, WILLIAM DUNLOP, 1810–1893

Alden, 53; *Brewer*, 555; *Britten*, 42; *DAB; Ewan*, 168; *Hughes*, 15; *Meisel*, 1:167 and 3:542; *Van Steenis*, 74–75; D. C. Haskel, U. S. Exploring Expedition, 1838–1842, and its publications, 1844–1874. New York, 1942 A. B. Maloney in Calif. Hist. Soc. Quart., 24:321–325 (portr.), 1945; A. Eastwood, *ibid.*, 337–342, 1945 H. H. Bartlett in Proc. Amer. Philos. Soc., 82:673–679, 1940.

BRANDEGEE, MARY KATHERINE LAYNE CURRAN, 1844–1920

DAB; W. A. Setchell in Univ. Calif. Publ. Bot., 13:165–168 (portr.), 1926; M. E. Jones, Contr. West. Bot., 18:12–18 (portr.), 1933.

BRANDEGEE, TOWNSHEND STITH, 1843–1925

DAB; Ewan, 170; *NCAB*, 23:366–367 (portr.); *Piper*, 18; W. A. Setchell in Univ. Calif. Publ. Bot., 13:155–178 (portr.), 1926; M. E. Jones, Contr. West. Bot., 15:15–18, 1929; J. Ewan in Amer. Midl. Nat., 27:772–789, 1942.

BRANNAN, SAMUEL, JR.

Cf. A. Kellogg in Proc. Calif. Acad. Sci., 5:16 (Feb. 3) and 5:39 (Mar. 3), 1873.

BREWER, WILLIAM HENRY, 1828–1910

Badè, 2:321; *Brewer*, 558; *Brewster*, 190–192; *DAB; Ewan*, 170; *Farquhar's Brewer*, introd., xv–xxx; *Howell*, 31; *Hultén*, 315; *NCAB*, 13:561 (portr.); *Sargent*, 8:28; E. H. Jenkins in Amer. Jour. Sci., ser. 4, 31:71–74, 1911; R. H. Chittenden in Nat. Acad. Sci. Biog. Mem., 12:289–323 (portr.), 1929.

BRIDGES, THOMAS, 1807–1865

Brewer, 558; *Britten*, 45; *Jepson*, 2:84–88, 1933; *Meisel*, 3:726 *s.v.* "Brydges, Thomas"; A. Gray in Amer. Jour. Sci., ser. 2, 41:265, 1866; I. M. Johnston in Contr. Gray Herb., 81:98–106, 1928; W. H. Dall, "Memorial sketch. . . read before the California Academy of Natural Sciences, Jan. 8th, 1866," pp. n.d., examined in N. Y. Bot. Garden Library.

BRUCE, (MRS.) C. C.

Cf. A. Eastwood in Bull. Torrey Bot. Club, 30:494, 1903.

BRYANT, HAROLD CHILD, 1886–

Amsci.

BRYANT, WALTER [PIERCE] E., 1861–1905

Palmer, 271; W. K. Fisher in Condor, 7:128–131 (portr.), 1905, and in Auk, 22:439–441, 1905; H. H. Bailey in Auk, 23:369–376, *passim*, 1906; H. W. Henshaw in Condor, 22:59, 1920.

BURBANK, LUTHER, 1849–1926

DAB; Fairchild, 263–265 *et passim* (portr.); *NCAB*, 33:149–150; *Woodcock & Stearn*, 171; J. Y. Beaty in Nature Mag., 42:309–311 (portr.), 1949, and in Flower Grower, 36:363 *et seq.* (portr.), April, 1949; W. L. Howard in Science Digest, 20:9–11, Nov. 1946; H. De Vries in Pop. Sci. Mo., 67:329–347, 1905; W. L. Howard, Luther Burbank: a victim of hero worship, Chron. Bot., 9:300–508 (portr.), 1946.

BURKE, JOSEPH

Britten, 55; *Ewan*, 175; *Sargent*, 9:4; *Wagner-three*, 144 refers to Dr. Elijah White meeting [erroneously "Dr."] Burke near Ft. Hall; Burke evidently shipped his colls. to England from San Francisco.

BURTT-DAVY, JOSEPH, 1870–1940

Bradley Bib., 5:213 *s.v.* Davy, Joseph Burtt; *Howell*, 31; J. Hutchinson in Nature, 146:424, 1940.

Butler, George Dexter, 1850–1910

Jepson, 1:188–190 (portr.); S. B. Parish, Biog. Bot., Vol. 1, Ms in Dept. Bot. Library, Pomona College.

Campbell, Douglas Houghton, 1859–1953

Amsci; D. S. Jordan, Days of a Man, 1:294, 398 (portr.), 1922; I. L. Wiggins in Amer. Fern Jour., 43:97–103, 1953.

Cannon, Evelina

Cf. A. Eastwood in Leafl. West. Bot., 4:154, 1945 and 5:45–46, 1947.

Carriger, Henry Ward

Cf. Pac. Coast Avifauna, 16:175, 1924 for his papers.

Chamisso, Adelbert Ludwig von, 1781–1838

Alden, 21–27; *Brewer*, 554; *Eastwood*, 338; *Embacher*, 73; *Essig*, 619–620 (portr.); *Hultén*, 298; *Lasegue*, 371–373; *Urban Fl. Bras.*, 1:11–12; *Van Steenis*, 104 (portr.); A. C. Mahr, Visit of the *Rurik* to San Francisco in 1816, Stanford Univ. Publ. Hist. Econ. and Pol. Sci., 2(2):15–18 *et passim*, 1932; A. Eastwood in Leafl. West. Bot., 4:17–21, 1944; W. E. Safford in U. S. Nat. Herb. Contr., 9:28–29, 1905; T. I. Storer in Univ. Calif. Publ. Zool., 27:47–48 and 79–80, 1925; autobiog. notes in Reise um die Welt mit der Romanzoffischen Entdeckungs-Expedition in 1815–18, auf der Brigg *Rurik*, Capt. Otto Kotzebue, 2 vols., Leipzig, 1846, and later eds., e.g., Entdeckungsreise um die Welt, pp. 103–118, Munich, 1925.

Chesnut, Victor King, 1867–1938

Amsci, ed. 6; *Bradley Bib.*, 5:173; *Howell*, 31; *NCAB*, 13:295; Who Was Who in Amer.

Clark, Howard Walton, 1870-1941

Dean, 1:381; edit. obit. in Copeia, 1941:278–279 (portr.), 1941.

Cleveland, Daniel, 1838–1929

Brewer, 559; *Jepson*, 1:267–268 (portr.), 1929; H. L. Mason in Madroño, 4:67, 1937; cf. San Diego [Calif.] Union for July 22, 1921.

Collie, Alexander, (?)–1835

Alden, 30; *Brewer*, 554; *Britten*, 70; *Huxley's Hooker*, 1:106; *Lasegue*, 84–85; *Palmer*, 273; J. Grinnell in Univ. Calif. Publ. Zool., 38:303 *et passim*, 1932.

Collignon, Jean Nicholas, 1762–1788

Van Steenis, 113, 602; cf. *NBG*, *s.v.* Cels, J. M.; Monterey colls. made by Collignon grown at garden of Jacques Martin Cels, 1743–1806, near Paris (cf. Ventenat, Hort. Cels, pref., p. 2, 1800).

Cooper, James Graham, 1830–1902

Blankinship, 6; *Brewer*, 558; *DAB; Essig*, 588; *Ewan*, 187; *Hume*, 38–51; *Meisel*, 1:174; *Palmer*, 273; *Piper*, 17; *Sargent*, 1:30; *Wagner-three*, 262; anon. in Auk, 19:421–422, 1902; cf. Condor, 53:194 for overlooked papers in Calif. Farmer and Journ. Useful Sciences; W. H. Dall in Science, n.s. 16:268–269, 1902; H. W. Henshaw in Condor, 22:59, 1920; contributed chapter on zoology to Titus Fey Cronise's Natural Wealth of California, 1868.

Cordua, Theodor, 1796–1857

Cf. J. T. Howell in Leafl. West. Bot., 1:180–181, 1935; Memoirs of Theodor Cordua, the pioneer of New Mecklenburg in the Sacramento Valley, ed. and transl. by E. G. Gudde, Calif. Hist. Soc. Quart., 12(4):1–33, Dec. 1933.

Cormack, William Epps, 1796–1868

Bradley Bib., 1:309; F. A. Bruton in Journ. Bot., 66:175–176, 1928; cf. Narrative of a Journey Across the Island of Newfoundland in 1822 St. Johns, 1824, which contains a list of about 170 plants taken in Newfoundland; map of route publ. in 1824 in Edinburgh Philos. Journal, 10:156–162; Cormack was a tobacco grower in Australia, forester in New Zealand, collector in California, and founder of agricultural society in British Columbia.

COULTER, THOMAS, 1793–1843

Alden, 38–39; *Brewer*, 74; *Britten*, 74; *Eastwood*, 341; *Stillman*, 319; F. V. Coville in Bot. Gaz., 20:519–531, map, 1895; R. McVaugh in Journ. Wash. Acad. Sci., 33:65–70, 1943; R. Lloyd Praeger, Some Irish Naturalists, 68, 1949; E. P. Wright in Notes from the Botanical School of Trinity College, Dublin, no. 1, pp. 3–4, 1896.

COUTHOUY, JOSEPH PITTY, 1808–1864

Dall, 72 and 80; *Meisel*, 1:175 and 3:557; H. H. Bartlett in Proc. Amer. Philos. Soc., 82:650–655, 1940.

CRUM, ETHEL KATHERINE, 1886–1943

H. L. Mason in Madroño, 7:33–35, 1943.

CURRAN, M. K., *see* BRANDEGEE, M. K. L. C.

DALL, WILLIAM HEALEY, 1845–1927

H. A. P[ilsbry] in Nautilus, 41:1–6, 1927; C. H. Merriam in Science, 65:345–347, 1927.

DANA, JAMES DWIGHT, 1813–1895

DAB, *Meisel*, 1:176–177 and 3:560; *NCAB*, 6:462 (portr.); *Van Steenis* 129; H. H. Bartlett in Proc. Amer. Philos. Soc., 82:655–663, 1940; F. S. Collins in Rhodora, 14:66 *et passim*, 1912; D. C. Gilman, Life of James Dwight Dana, 1899; L. V. Pirsson in Nat. Acad. Sci. Biog. Mem., 9:41–92 (portr.), 1919.

DAVIDSON, GEORGE, 1825–1911

DAB, *NCAB*, 7:227 (portr.) ; C. B. Davenport in Nat. Acad. Sci. Biog. Mem., 18:189–217 (portr.), 1938.

DELATTRE, PIERRE ADOLPHE, 1805–1854

J. Grinnell in Univ. Calif. Publ. Zool., 38:262, 1932; T. S. Palmer in Condor, 20:123–124, 1918.

DE MOFRAS, EUGENE DUFLOT, *see* DUFLOT DE MOFRAS, EUGENE

DEPPE, FERDINAND, 1794–1867

Alden, 39; *Brewer*, 555; *Lasegue*, 468; H. Harris in Condor, 43:23–27, 1941; autobiog. notes in Reisen in Kalifornien, Lüdde, Zeitschr. f. Erdkunde, 7:383–390, 1847, not seen. The death year "1828" cited by Chittenden, Dict. of Gardening, 1951, is an error.

DOANE, RENNIE WILBUR, 1871–1942

Carpenter, 24; W. M. Mann, Ant Hill Odyssey, 68, 1948.

DOUGLAS, DAVID, 1799–1834

Alden, 32–37 (portr.); *Blankinship*, 5; *Brewer*, 554; *Britten*, 94; *Candolle*, 408; *Douglas*, 9; *Eastwood*, 339; *Ewan*, 197; *Geiser-two*, 273; *Howell*, 29; *Lasegue*, 193–196; *Meisel* 1:179 and 3:729; *Palmer*, 276; *Piper*, 12–13; *Stillman*, 317–319; *Wagner-three*, 60; cf. L. Constance in Leafl. West. Bot., 2:21–22, 1937; H. Harris in Condor, 43:19–21, 1941; J. T. Howell in Leafl. West. Bot., 3:160–162, 1942; W. L. Jepson in Madroño, 2:97–100, 1933; E. L. Little, Jr., in Phytologia, 2:485–490, 1948; portr. in Appalachia, 13:54, 1913.

DREW, ELMER REGINALD, 1865–1930

Amsci, ed. 4; *Howell*, 31.

DUDLEY, WILLIAM RUSSEL, 1849–1911

Bradley Bib., 5:240; *DAB;* various authors in Dudley Memorial Volume, Stanford Univ. Publ., 5–28 (portr.), 1913; D. S. Jordan, Days of a Man, *passim*, 1922.

Duflot de Mofras, Eugene, 1810–1884

Hughes, 17; *NBG; Sabin*, 21144; *Stillman*, 325; cf. M. E. Wilbur, Duflot de Mofras Travels on the Pacific Coast, 2 vols., Santa Ana, Calif., 1937.

Dufresne, Louis

Sherborn; cf. M. Deleuze, Histoire et Description du Museum Royal d'Historie Naturelle, 1:169–170, 1823.

Dunn, George Washington, 1814–1905

Essig, 605 *et passim; Jepson*, 2:156–157 (portr.), 1934.

Eastwood, Alice, 1859–1953

Ewan, 200; *Fairchild*, 444; *Howell*, 31; L. R. Abrams in Pac. Discovery, 2(1):14–17 (portrs.), 1949; cf. Acad. News Letter no. 36 (portr.), Dec., 1942; E. Crum in Madroño, 5:74 (portr.), 1939; M. E. Jones, Contr. West. Bot., 18:8, 1933 (portr.); cf. Leafl. West. Bot., 4:153–156, 1945 for recollections; R. C. Miller in Golden Gardens, 9(12):3–4, 15 (portr.), 1941; N. Valjeans in Nature Mag., 42:361–362 (portr.), 1949; editorial in Sunset for Feb., 1938, pp. 13–15 (portr.); San Francisco Chronicle for Oct. 31, 1953 (portr.).

Eaton, Amos Beebe

Brewer, 558.

Edwards, Henry, 1830–1891

Badè 1:262–264 *et passim; Carpenter*, 27; *Essig*, 611–613 (portr.); *Ewan*, 201; *Musgrave*, 76; *Osborn*, 1:162; edit. obit. in Entom. News, 2:129–130 (portr.), 1891; J. S. Wade in Sci. Mo., 30:240–250, 1930.

Eisen, Gustavus Augustus, 1847–1940

Bradley Bib., 5:254; *Carpenter*, 28; *Essig*, 615–617 (portr.); A. B. Benson and N. Hedin, Americans from Sweden, 295, 1950; L. H. Miller, Lifelong Boyhood, 77, 1950; Edgar Swenson in Amer. Swedish Mo. for Nov., 1935.

Emerson, William Otto, 1856–1940

T. S. Palmer in Auk, 65:492–493, 1948; portr. in Condor, 39:46, 1937.

Eschscholtz, Johann Friedrich, 1793–1831

Alden, 27–28; *Brewer*, 554; *Carpenter*, 29; *Embacher*, 108; *Essig*, 617–622 (portr.); *Howell*, 29; *Lasegue*, 212–213; *Musgrave*, 83; *NBG; Van Steenis*, 157, as "Eschscholz"; A. Eastwood in Leafl. West. Bot., 4:17–21, 1944; W. L. Jepson in Madroño, 1:253 (portr.), 1929. W. E. Safford in U. S. Nat. Herb. Contr., 9:28–29, 1905.

Evermann, Barton Warren, 1853–1932

DAB, Suppl. One; *Dean*, 1:377–383; *Ewan*, 206; *Hultén*, 309; *NCAB*, 13–570 (portr.); D. S. Jordan, Days of a Man, 1:169 *et passim*, 1922; T. S. P[almer] in Auk, 50:465–466, 1933; G D. Hanna in Copeia, no. 4:161–162 (portr.), 1932; San Francisco Chronicle for Sept. 28, 1932; autobiog. note in Proc. Indiana Acad. Sci., 1916:209–210, 1916.

Farris, Charles

R. C. Miller in Pacific Discovery, 6(2):19–20, 1953.

Feilner, John

Cf. J. Grinnell in Pac. Coast Avifauna, 5:20, 1909; cf. Nineteenth Ann. Rept. Smithson. Inst. (for 1864), 421–430, 1865.

Fischer. Friedrich Ernst Ludwig von, 1782–1854

Bradley Bib., 5:281; *Essig*, 630.

Fisher. Walter Kenrick, 1878–1953

Amsci: D. S. Jordan, Days of a Man, 2:130 *et passim*, 1922; autobiog. notes in Condor, 42:35–38, 1940.

FITCH, AUGUSTUS

Bradley Bib., 5:282; *Meisel*, 3:574; cf. J. Torrey in Pac. RR. Repts., 4:109, 1857.

FRÉMONT, JOHN CHARLES, 1813–1890

Brewer, 556; *DAB; Ewan*, 211; *Hughes*, 17; *Meisel*, 1:184–185 and 3:577, 730; *NCAB*, 4:270–272 (portr.); *Wagner-three*, 95, 115; G. A. Zabriskie in N. Y. Hist. Soc. Quart., 31:4–17 (portr.), 1947.

FROEBEL, JULIUS, 1805–1893

Embacher, 122; *Geiser-two*, 274; *Meisel*, 3:577; *NBG*, b. "1806"; *Wagner-three*, 292; A. E. Zucker, Forty-eighters, 295, 1950; Aus Amerika. Erfahrungen, Reisen und Studien, 2 vols., Leipzig, 1857–1858, in transl. as Seven Years' Travel in Central America, Northern Mexico and the Far West of the United States, London, see esp. 570–578, 1859, and as À Travers l'Amérique, 3 vols., Brussels, 1861.

FUCHS, CARL, 1839–1914

Carpenter, 34; *Essig*, 635–637 (portr.); W. M. Mann, Ant Hill Odyssey, 79, 1940.

FUNSTON, FREDERICK, 1865–1917

DAB; Hultén, 309; *NCAB*, 11:40–41 (portr.); D. S. Jordan, Days of a Man, 1:317 and 2:177, 1922; autobiog. Memories of Two Wars: Cuban and Philippine Experiences, 1911, "a vigorous and unconventional narrative"; cf. V. Bailey, Into Death Valley fifty years ago, Westways, 32 (no. 12, pt. 1):8–11 (portrs.), Dec., 1940.

GABB, WILLIAM MORE, 1839–1878

Brewster, 239 and 256; *DAB; Essig*, 638; W. H. Dall in Nat. Acad. Sci. Biog. Mem., 6:347–361 (portr.), 1909; edit. obit. in Amer. Nat., 12:494–495, 1878.

GAMBEL, WILLIAM, 1821–1849

Brewer, 556; *Ewan*, 213; *Harshberger*, 231–233; *Meisel*, 1:185; *Palmer*, 278; *Sargent*, 8:35; *Stone*, 11–12; J. Grinnell in Univ. Calif. Publ. Zool., 38:316 *et passim*, 1932; H. Harris in Condor, 43:35, 1941; C. F. Millspaugh and L. W. Nuttall, Flora of Santa Catalina Island, 28, 1923; W. Stone in Cassinia, 14:1–8, 1910; D. B. Woods in Amer. Journ. Sci., ser. 2, 11:143–144, 1851.

GARDNER, NATHANIEL LYON, 1864–1937

Amsci, ed. 5; D. S. Jordan, Days of a Man, 1:302, 1922; W. A. Setchell in Madroño, 4:126–128 (portr.), 1937.

GARMAN, SAMUEL, 1843–1927

DAB; Ewan, 214; *NCAB*, 10:294.

GARVITT, ——?

Brewer, 557.

GIBBONS, HENRY, 1808–1884.

Meisel, 1:186; *NCAB*, 7:287–288 (portr.); R. C. Miller in Pacific Discovery, 6(2):18–25 (portr.), 1953.

GIBBONS, WILLIAM PETERS, 1812–1897

Bradley Bib., 5:320; *Badè*, 2:70; *Dean*, 1:457; *Kelly*, 216; *Meisel*, 1:186; W. L. Jepson in Erythea, 5:74–76, 1897; author of Waysides of Nature, I, II, and III, Overland Mo., Aug. 1870 and Aug., 1875.

GIBBS, C. [or G?] D.

Bradley Bib., 4:527; *Brewer*, 557; cf. P. A. Munz in Leafl. West. Bot., 7:69, 1953, as "C. D. Gibbes at Stockton."

GIBBS, GEORGE, 1815–1873

ACAB, s.v. Geo. Gibbs, his father; *DAB; Dall*, 338; *Meisel*, 1:187; S. F. Baird in

Ann. Rec. Sci. and Indust. for 1873, 683, 1875; Biog. sketch in folder Oregon Biog. (A–Z) at Bancroft Library, Berkeley; G. P. Fisher, Life of Benj. Silliman, 1:214 *et passim*, 1866.

Gilbert, Charles Henry, 1859–1928

Amsci, ed. 4; *Dean*, 1:459–461; D. S. Jordan, Days of a Man, 1:201–229 *et passim* (portr. opp. p. 140), 1922; W. M. Mann, Ant Hill Odyssey, 69–70 and 81, 1948.

Goddard, Pliny Earle, 1869–1928

Amsci, ed. 4; Who Was Who in Amer.; F. Boas in Science, 68:149–150, 1928; A. L. Kroeber in Amer. Anthro., 31:1–8 (portr.), 1929.

Goodale, George Lincoln, 1839–1923

Amsci, ed. 3; *Bradley Bib.*, 5:331; *DAB; Meisel*, 3:730; B. L. Robinson in Pop. Sci. Mo., 39:691–694 (portr.), 1891; W. Trelease in Science, n.s., 57: 654–656, 1923; L. H. Bailey in Rhodora, 25:117–120 (portr.), 1923; W. J. V. Osterhout, B. L. Robinson, and M. L. Fernald in Amer. Journ. Sci., ser. 5, 6:275–276, 1923.

Goodridge, J.

Cf. B. Seemann, Botany of the "Herald," 286, 1852; Frederick Scheer named a cactus of Cedros Island *Mamillaria goodridgii* for the ship's surgeon attending the "Herald" but his collecting activities in this region were evidently negligible.

Gordon-Cumming, Constance Frederica, 1837–1924

Bradley Bib., 1:320, *s.v.* "Cumming, C. F. G."; cf. her autobiog. acct. Granite Crags. Edinburgh and London, 1884.

Gray, Asa, 1810–1888

ACAB; DAB; Ewan, 218; *Harshberger, passim; Huxley's Hooker*, 2:210–218; *Kelly*, 165–177 (portr.); *Meisel*, 1:188–189; *NCAB*, 3:407–408 (portr.); *Rodger's Gray*, 131–143 *et passim; Badè, passim;* G. Bradford in N. Amer. Rev., 215:99–108, 1922; H. H. Bartlett in Proc. Amer. Philos. Soc., 82:664–673, 1940.

Grayson, Andrew Jackson, 1819–1869

Palmer, 279–280; W. E. Bryant in Zoe, 2:34–68, 1891; L. C. Taylor in Condor, 53:194–197, 1951; H. Harris in Condor, 43:31–32, 1941.

Greene, Edward Lee, 1843–1915

Brewer, 559; *DAB; Ewan*, 219; *NCAB*, 19:332–333; K. B(randegee) in Zoe, 2:88–89, 1891; P. L. Ricker in Science, n.s., 39:109–112, 1914; A. K. Main in Trans. Wis. Acad. Arts and Letters, 24:147–185, 1929; H. H. Bartlett in Torreya, 16:151–175 (portr.), 1916; W. L. Jepson in Newman Hall Rev. for Oct. 1918; Amer. Catholic Who's Who, 256, 1911; M. E. Jones, Contr. West. Bot., 14:49–50, 1912, and 15:25–27, 1929; Jack Barber in Catholic World, 160:444–449, Feb., 1945.

Grinnell, Joseph, 1877–1939

Palmer, 280–281; J. M. Linsdale in Auk, 59:269–285 (portr.), 1942; Hilda Wood Grinnell in Condor, 42:3–34 (portrs.), 1940; W. K. Fisher, *ibid.* 35–38 (portr.), 1940; F. B. Sumner, Life History of an American Naturalist, 213–217, 1945; J. Mailliard in Condor, 26:16, 1924; A. H. Miller in Joseph Grinnell's Philosophy of Nature, pref., vii–x, (frontis. portr.), 1943.

Gruber, Ferdinand, 1830–1907

Palmer, 281; H. W. Henshaw in Condor, 22:59, 1920; cf. J. Grinnell in Univ. Calif. Publ. Zool., 38:263, 315 *et passim*, 1932; cf. Condor, 53:194 for overlooked papers in serial Calif. Farmer and Journ. Useful Sci.

Haenke, Thaddeus, 1761–1817

Alden, 13; *Brewer*, 553; *Eastwood*, 336; *Hultén*, 297; *Lasegue*, 451; *NBG; Van Steenis*, 209–210; W. L. Jepson in Erythea, 7:129–134, 1899; E. C. Galbraith in Calif. Hist. Quart., 3(3):215–237, 1924; W. E. Safford in U. S. Nat. Herb. Contr., 9:25–28, 1905.

HALL, CARLOTTA CASE, 1880–1949

Cf. Amer. Fern. Journ., 40:192, 1950; Madroño, 4:283, 1938.

HALL, HARVEY MONROE, 1874–1932

Ewan, 222; E. B. Babcock in Univ. Calif. Publ. Bot., 17:355–368 (portr.), 1934; W. L. J(epson) in Madroño, 2:63, 1932; portr. in Madroño, 1:12, 1916.

HANNA, G DALLAS, 1887–

Amsci: Hultén, 331; D. S. Jordan, Days of a Man, 1:551 *et passim*, 1922; initial does not stand for a name, *teste* Condor, 33:210.

HANSEN, GEORGE, 1863–1908

Bradley Bib., 5:364; *DAB; Jepson*, 1:183–185 (portr.), 1928.

HARFORD, WILLIAM G. W., 1825–1911

Brewer, 556; *Essig*, 650; *Jepson*, 2:83–84 (portr.), 1933; D. S. Jordan, Days of a Man, 1:218, 1922; W. H. D[all] in Nautilus, 25:8, 1911.

HARKNESS, HARVEY WILLSON, 1821–1901

Cf. *Essig*, 740, *s.v.* Ricksecker; Who Was Who in Amer.; [T. S. Brandegee in] Zoe, 2:1–2 (portr.), 1891.

HARTWEG, KARL THEODORE, 1812–1871

Alden, 47–48; *Brewer*, 556; *Britten*, 141; *Eastwood*, 342; *Howell*, 29; *Lasegue*, 207–209; *Sargent*, 2:34; *Urban Symb. Ant.*, 57; J. T. Howell in Leafl. West. Bot., 1:180–181. 1935; W. L. Jepson in Erythea, 5:31–35, 51–56, 1897.

HEATH, HAROLD, 1868–

Amsci: Dean, 1:555; W. M. Mann, Ant Hill Odyssey, 69, 1948.

HEERMANN, ADOLPHUS LEWIS, 1827–1865

Brewer, 557; *Dall*, 280–281; *Geiser-two*, 275; *Hume*, 190–205 (portr.), best account; *Meisel*, 3:732; *Palmer*, 282; *Stone*, 13; H. Harris in Condor, 43:35–36, 1941.

HELLER, EDMUND, 1875–1939

Ewan, 226; *Hultén*, 322; Who Was Who in Amer.; D. S. Jordan, Days of a Man, 2:421, 1922.

HEMPHILL, HENRY, 1830–1914

W. H. Dall in Science, 40:265–266, 1914, and in Nautilus, 28:58–59, 1914; cf. B. W. Evermann in Nature and Science on the Pacific Coast, 208, 1915; obit. in Trans. San Diego Soc. Nat. Hist., 2:58–60 (portr.), 1914.

HENSHAW, HENRY WETHERBEE, 1850–1930

Palmer, 282; D. S. Jordan, Days of a Man, 2:90, 1922; E. W. Nelson in Auk, 49:399–427 (portr.), 1932; T. S. Palmer in Auk, 47:600–601, 1930; autobiography in Condor, 21:102–107 (portr.), 165–171 (portr.), 177–181, 217–222, 1919, and 22:3–10, 55–60, 95–101, 1920.

HEPBURN, JAMES, 1811–1869

Cf. T. S. Palmer in Condor, 33:221, 1931; H. S. Swarth in Condor, 28:249–253, 1926.

HERRE, ALBERT WILLIAM CHRISTIAN THEODORE, 1868–

Amsci; Who's Who in Amer.

HICKMAN, JOHN BALE, fl. 1880–1900

Bradley Bib., 5:391.

HILGARD, EUGENE WOLDEMAR, 1833–1916

Bradley Bib., 5:392–393; *DAB; Fairchild*, 444; R. M. Harper in Bull. Torrey Club 43: 389–391, 1916; F. Slate in Nat. Acad. Sci. Biog. Mem., 9:95–155 (portr.), 1919.

Hillebrand, William, 1821–1886

ADB; Brewer, 558; *Van Steenis*, 232 (portr.); A. Gray in Amer. Journ. Sci., ser. 3, 33:164–165, 1887; H. St. John in Chron. Bot., 7:69–70, 1942; cf. E. T. Allen in Science, 74:60–62, 1931; autobiog. notes in Fl. Haw. Isl., pref., vii–xii, 1888.

Hinds, Richard Brinsley, 1812?–1847

Alden, 46; *Brewer*, 555; *Britten*, 149; *Sherborn; Van Steenis*, 232.

Holden, E. S.

J. Grinnell in Univ. Calif. Publ. Zool., 38:273, 300–301, 1932, refers to Stockton colls.; *Dean*, 1:594, refers to "E. C. Holden" who may be same person but D. S. Jordan, Days of a Man, 1:392, 1922, refers to E(dward) S(ingleton) Holden, 1846–1914, astronomer of Lick Observatory (cf. Who Was Who in Amer. and *Amsci*, ed. 2), who can scarcely be same person though his interests were diverse.

Holder, William

Brewer, 558; see C. F. Holder's Holders of Holderness (n.d.).

Holmes, Frank Henry, 18—?–1924

T. S. Palmer in Condor, 33:221, 1931.

Hooker, Joseph Dalton, 1817–1911.

Badè, passim; Britten, 152–153; *DNB*, suppl. 2, 2:294; *Ewan*, 233; *Gray*, 672–675 for Calif. trip of Aug., 1877; *Huxley's Hooker*, 205–218; Rewa Glenn, Botanical Explorers of New Zealand, 81–86, 1950; D. Prain in Ann. Rept. Smith. Inst., for 1911, 659–671 (portr.), 1912; B. L. Robinson in Proc. Amer. Acad. Arts and Sci., 62:257–266, 1928.

Horn, George Henry, 1840–1897

Brewer, 558; *Carpenter*, 46; *DAB; Essig*, 654–658 (portr.); *Meisel*, 1:196; *NCAB*, 7:502–503; J. B. Smith in Science, n.s., 7:73–77, 1898, and in Pop. Sci. Mo., 76:468–469, 1910; edit. obit, in Entom. News, 9:1–3 (portr.), 1898.

Howell, John Thomas. 1903–

Amsci; Ewan, 236.

Hudson, Charles Bradford, 1865–

Artist of Academy's diorama backgrounds; Benezit, Dictionnaire critique . . . peintres, 1952; D. S. Jordan, Days of a Man, 2:87, 1922, as "Charles Bradley Hudson"; Who's Who in American Art, A. C. McGlauflin, ed., 1:211, 1935.

Hutchings, James Mason, 1818–1902

Badè, passim; Farquhar's Yosemite, 18–21, 73–77; F. Walker, San Francisco's Literary Frontier, 28 *et passim*, 1939.

Jeffrey, John, 1826–1854

Brewer, 557; *Britten*, 165; *Eastwood*, 343; *Hughes*, 19; *Meisel*. 3:733; F. V. Coville in Proc. Biol. Soc. Wash., 11:57–60, 1897; J. T. Johnstone in Notes from Roy. Bot. Gard. Edinburgh, 20:1–53, 1939.

Jepson, Willis Linn, 1867–1946

D. D. Keck in Madroño, 9:223–228, 1948, where a bibliog. of biog. refs, is given. To Keck's list may be added: H. D. Carew in Touring Tropics, 20(12):32–34, 50 (portr.), Dec., 1928; obit, in Carnegie Found. for Adv. Teaching, 42nd Ann. Rept. (1946–47), pp. 79–80, 1947; H(elen) M(arr) Wheeler in Desert Plant Life, 19:43–45, March, 1947. Cf. also San Francisco Examiner for Nov. 8, 1946, p. 15; San Francisco Chronicle for Nov. 8, 1946, p. 11 and Nov. 9, 1946, p. 7; *Howell*, 31; autobiog. notes in Madroño, 4:276–286 (frontis. portr.), 1938.

Jones, Katherine Davies, 1860–1943

M. Symmes in Madroño, 8:184–187, 1946.

JORDAN, DAVID STARR, 1851–1931

DAB; Dean, 1:643–661; *Ewan*, 241; *NCAB*, 22:68–70 (portr.); B. W. Evermann in Proc. Indiana Acad. Sci., 1916:205–207, 1916; B. W. Evermann in Condor, 34:6–7, 1932, on his interest in birds; H. Zinsser, As I Remember Him, the Biography of R. S., 188–194, 1940; autobiog. Days of a Man, 2 vols., 1922; W. M. Mann, Ant Hill Odyssey, 67–81, 1941; T. D. A. Cockerell in Pop. Sci. Mo., 62:516, 1903.

JORDAN, ERIC KNIGHT, 1903–1926

Anon. in Nautilus, 40:33–34, 1926.

KAEDING, HENRY BARROILHET, 1877–1913

Palmer, 283; J. Mailliard in Condor, 15:191–193 (portr.), 1913.

KEEP, JOSIAH, 1849–1911

Author of Common Seashells of California, ed. 1, 64 pp., 1881, and West Coast Shells, 230 pp. 1887; W. H. Dall in Science, 34:371, 1911, and Nautilus, 25:61–62 (portr.), 1911.

KELLEY, LYNWOOD J.

Woodcock & Stearn, 244.

KELLOGG, ALBERT, 1813–1887

Badè, 2:70 *et passim; Bradley Bib.*, 5:449–450; *Brewer*, 556; *DAB; Essig*, 650 *et passim; Geiser-two*, 276; *Hulten*, 302; *Meisel*, 1:200 and 3:734; *NCAB*, 25:205–206; *Wagner-three*, 274a; *Woodcock & Stearn*, 245; A. Gray in Amer. Journ. Sci. ser. 3, 35:261–262, 1888; E. L. Greene in Pittonia, 1:145–151, 1887; D. S. Jordan, Days of a Man, 1:218, 1922; R. C. Miller in Pacific Discovery, 6(2):18–25 (portr.), 1953; P. A. Munz in Leafl. West. Bot., 7:70–71, 1953; cf. Leafl. West. Bot., 7:101 (pl. 5), 1953, for his handwriting; C. H. Shinn in Garden and Forest, 2:298, 1889.

KELLOGG, VERNON LYMAN, 1867–1937

Amsci, ed. 5; *Carpenter*, 51; L. O. Howard, Fighting the Insects, 188, 1933; D. S. Jordan, Days of a Man, *passim*, 1922; C. E. McClung in Nat. Acad. Sci. Biog. Mem., 20:245–257 (portr.), 1939; W. M. Mann, Ant Hill Odyssey, 68–69, 1948; Who was Who in Amer.

KENNEDY, PATRICK BEVERIDGE, 1874–1930

W. L. Jepson in Madroño, 2:34–35 (portr.), 1931; cf. Bot. Soc. Amer. Publ. 105, 19–20, 1931.

KING, CLARENCE, 1842–1901

Badè, passim; DAB; Farquhar's Brewer, passim; Farquhar's Yosemite, 49–53; *Meisel*, 1:201; S. F. Emmons in Nat. Acad. Sci. Biog. Mem., 6:25–55 (portr.), 1909; cf. his Mountaineering in the Sierra Nevada, 1871.

KNOCHE, EDWARD LOUIS HERMAN, 1870–

Dudley Memorial Volume, 31, 1913, in list of Dudley's students; cf. Madroño, 4:283, 1938.

KOFOID, CHARLES ATWOOD, 1865–1947

C. Dobell in Nature, 160:115–116, 1947; R. B. Goldschmidt in Nat. Acad. Sci. Biog. Mem., 26:121–151 (portr.), 1951; H. Kirby in Sci. Mo., 61:415–418 (portr.), 1945 and in Science, 106:462–463, 1947; portr. in Fortune, 33(6):157, 1946.

KOTZEBUE, OTTO VON, 1787–1846

Brewer, 554; *Embacher*, 176; *Lasegue*, 371; *NBG; Palmer*, 284; *Stillman*, 310–316.

LAGLAIZE, LÉON

A. Boucard, Travels of a Naturalist, 50, 1894; "grandson of Lorquin" who collected insects in San Francisco region during the 1850's.

Langsdorff, Georg Heinrich von, 1774–1852

Alden, 19–21; *Brewer*, 554; *Howell*, 29; *Hultén*, 297; *NBG; Stillman*, 308; *Swainson*, 231.

Lanszweert, L.

Dean, 2:12, who cites one paper.

La Pérouse, Jean Francois Galaup de, 1741–1788

Alden, 9–12; *Eastwood*, 335; *Embacher*, 182; *NBG; Stone*, 4; G. Chinard, Le Voyage de Lapérouse sur les côtes d l'Alaska et de la Californie (1786), esp. p. 106, 1937; cf. M. Gabriel Marcel, bibliog. of La Pérouse in Bull. Soc. Geog. France for 1888.

Lathrop, Barbour, 1846–(?)

Fairchild, 104, 302, *et passim* (portr., 84A); D. Fairchild, Exploring for Plants, 328 *et passim*, 1930; and World Grows Round My Door (portr.), 73 *et passim*, 1947; M. S. Douglas in Reader's Digest, 53:67–71 (portr.), Nov., 1948.

Lay, George Tradescant, (?)–1845.

Alden, 30–31; *Brewer*, 534; *Britten*, 182; *Lasegue*, 84–85; *Van Steenis*, 315–316; cf. Notes and Queries, ser. 1, 5:386, 1852.

LeConte, John Lawrence, 1825–1883

Carpenter, 58; *DAB; Essig*, 680–685; *Ewan*, 248; *Meisel*, 1:203–204; *Palmer*, 285; G. H. Horn in Science, 2:783–786, 1883; S. H. Scudder in Nat. Acad. Sci. Biog. Mem., 2:261–293, 1886; J. B. Smith in Pop. Sci. Mo., 76:468–469 (portr.), 1910.

LeConte, Joseph, 1823–1901

Badé, *passim; DAB; Farquhar's Yosemite*, 58; *Meisel*, 1:204; E. W. Hilgard in Nat. Acad. Sci. Biog. Mem., 6:147–218 (portr.), 1909; D. S. Jordan, Days of a Man, *passim*, 1922; L. H. Miller, Lifelong Boyhood, 104–105, 1950; cf. Autobiography of Joseph LeConte, ed. by W. D. Armes, 1903; cf. his A Journal of Ramblings Through the High Sierras of California by the University Excursion Party (1875), reprinted by Sierra Club, 1900; cf. his Flora of the Coast Islands of California in Relation to Recent Changes of Physical Geography, Bull. Calif. Acad. Sci., 8:515–520, 1887.

Lemmon, John Gill, 1832–1908

Brewer, 558; *DAB; Ewan*, 249; H. F. Copeland in Madroño, 5:77 (portr.); mss. notes in Ewan files; Harold St. John is preparing an account of J. G. Lemmon (cf. Berkeley Gazette for June 9, 1941) the "Professor" in Mabel Craft Deering's story "Kidnaping the Casting Vote" (Sunset Mag., 16:371–378, Feb., 1906) is Lemmon, *fide* S. B. Parish in mss. Biog. Bot., Vol. 2, Dept. Bot. Lib. Pomona Coll.

Letcher, Beverly, 1864–1905

Essig, 636 (portr.).

Lobb, William, 1809–1863

Brewer, 557; *Britten*, 191; *Eastwood*, 343; *Sargent*, 10:60; Veitch's account reprinted by A. Eastwood in Muhlenbergia, 7:100–103, 1911; cf. A. Eastwood in Leafl. West. Bot., 5:155–156, 1949; cf. *Farquhar's Yosemite*, 5–13, for survey of early literature on Big Tree but no mention of Lobb.

Lockington, William Neale, 1842(?)–1902

Dean, 2:52–53; D. S. Jordan, Days of a Man, 218, 1922.

Loomis, Leverett Mills, 1857–1927

L. B. Bishop in Auk, 46:1–13 (portr.), 1929; T. S. Palmer in Auk, 45:263–264, 1928; H. S. S(warth) in Condor, 30:194–195, 1928.

Lorquin, Pierre Joseph Michel, 1797–1873

Carpenter, 62; *Essig*, 694–697 (portr.); F. Grinnell, Jr., in Entom. News, 15:202–204, 1904, as "ca. 1800–1877"; cf. J. Grinnell in Univ. Calif. Publ. Zool., 38:318, 1932, and H.

Harris in Condor, 43:44, 1941; cf. H. W. Henshaw in Condor, 22:59, 1920, on Ernest F. Lorquin of "410 Kearney St., San Francisco."

LOTSY, JOHANNES PAULUS, 1867–1931

Van Steenis. 330–331 (portr.); A. D. Rogers, III, Erwin Frink Smith, 220–221, 1952; autobiog. notes in Van Den Atlantischen Oceaan naar de Stille Zuid Zee, Dagboek van een botanicus, die niet alleen naar planten keek. s-Gravenhage, esp., 288–294, 1930.

MCLAREN, JOHN, 1846(?)–1943

Bradley Bib., 5:534; *Fairchild*. 444, and World Grows Round My Door, 46 and 146, 1947; Samuel Dickson, San Francisco Is Your Home, 215–221, 1947; Frank J. Taylor in St. Eve. Post for July 29, 1939.

MCLEAN, F. P.

Collected plants on "stream of Tamalpais" in 1873 (cf. *Psoralea fruticosa* Kell.); (?) relative to Miss K. D. McLean of Oakland (cf. Cassino, Nat. Direct. for 1890).

MACKIE, WILLIAM WYLIE, 1873–

Cf. W. L. Jepson in Madroño, 4:276, 1938.

MAILLIARD, JOSEPH, 1857–1945

R. C. Miller in Auk, 64:300–302 (portr.), 1947; autobiog. in Condor, 26:10–29 (portr.), 1924.

MANN, HORACE, JR., 1844–1868

Brewer, 558; Wm. T. Brigham in Boston Soc. Nat. Hist. Proc., 12:152–155, 1868; "Friend and Associate" in Essex Inst. Bull., 1:25–31, 41–50, 1869.

MANN, WILLIAM M., 1886–

Amsci; autobiog. Ant Hill Odyssey, 1948 (portr.); Sci. Mo., 63:358 (portr.), 1946.

MARTINIÈRE, DE BOISSIEU LA

Alden, 11; *Van Steenis*, 350; cf. Vellozo, Fl. Flumin., 232, 1825, and Antoine Guillemin in Delessert, Icon. select., 3:23, t. 49, 1837.

MASON, HERBERT LOUIS, 1896–

Amsci; Howell, 31; *Hultén*, 338.

MCDONALD, JAMES MONROE, 1825–1907

Essig, 61 *et passim;* San Francisco Call for Feb. 28, 1892, and June 9, 1907; San Francisco Chronicle for Dec. 17, 1921.

MCGREGOR, RICHARD CRITTENDEN, 1871–1936

Dean, 1:657; *Palmer*, 287; obit. in Auk, 54:234, 1937; J. Grinnell in Auk, 55:163–175 (portr.), 1938; J. G(rinnell) in Condor, 39:45, 1937; D. S. Jordan, Days of a Man, 1:709, 1922.

MENZIES, ARCHIBALD, 1754–1842

Alden, 14–18 (portr.); *Brewer*, 553; *Britten*, 213; *Dean*, 2:129; *DNB; Hughes*, 7; *Hultén*, 297; *Lasegue*, 366; *Liverpool*, 61; *Jepson*, 1:262–266 (portr.), 1929; *Stone*, 4; A. Eastwood in Leafl. West. Bot., 2:92–94, 1938; J. Grinnell in Condor, 34:243–252, 1932; E. S. Meany, Vancouver's Discovery of Puget Sound, 295–297 *et passim* (portr.), 1915; Geo. Godwin, Vancouver: a Life, 1757–1798, 134–143 *et passim*, 1930; A. Eastwood in Calif. Hist. Soc. Quart., 2:265–340, 1924; Rewa Glenn, Botanical Explorers of New Zealand, 42–44, 1950.

MERRIAM, JOHN CAMPBELL, 1869–1945

Amsci. ed. 7; *NCAB*, Current Vol. A, 485–486 (portr).; *Palmer*, 288; Chester Stock in Science, 103:470–471, 1946, and in Geol. Soc. Amer. Proc., 1946:183–197 (portr.), 1947, and in Nat. Acad. Sci. Biog. Mem., 26:209–232 (portr.), 1951.

MEXIA, YNES ENRIQUETTA JULIETTA REYGADAS [née MEXIA], 1870–1938

N. Floy Bracelin (Mrs. H. P.) in Madroño, 4:273–275 (portr.), 1938; cf. Madroño, 4:284, 1938; H. N. Moldenke in Plant Life, 2(1–3):78, "1946" 1948; San Francisco News for Mar. 6, 1937 (portr.).

MICHENER, CHARLES A.

Howell, 31.

MUIR, JOHN, 1838–1914

DAB; Hultén, 304; W. F. Badè, Life and Letters of John Muir, 2 vols., 1923–1924; L. M. Wolfe, John Muir, 1838–1914, 15 pp. (n.d.) (brochure publ. by H. Mifflin Co.); D. S. Jordan, Days of a Man, 1:217, 1922; *s.v.* Edwards, Henry, *ante*.

NEBOUX, ADOLPHE SIMON, fl. 1836–1840

Palmer, 289; T. S. Palmer in Condor, 20:114–116, 1918; cf. J. Grinnell in Univ. Calif. Publ. Zool., 38:319–320, 1932.

NELSON, EDWARD WILLIAM, 1855–1934

W. S(tone) in Auk, 51:431–432, 1934; E. A. Goldman in Auk, 52:135–148 (portr.), 1935; V. Bailey in Westways, 32 (no. 12, pt. 1):8–11 (portr.), Dec., 1940; cf. Sci. Mo., 1:232–234, 1876, for birds of Oakland, Calif., *teste* E. Coues.

NEVINS, THOMAS J.

R. C. Miller in Calif. Hist. Soc. Quart., 21:364, 1942, and Pacific Discovery, 6(2):18–25, 1953.

NEWBERRY, JOHN STRONG, 1822–1892

Blankinship, 10; *Brewer*, 557; *DAB; Dean*, 2:179–181; *Ewan*, 272; *Hughes*, 20; *Meisel*, 1:214; C. A. White in Nat. Acad. Sci. Biog. Mem., 6:3–24 (portr.), 1909; N. L. Britton in Bull. Torrey Club, 20:89–98 (portr.), 1893.

NEWCOMB, WESLEY, 1808–1892

Brewster, 217; *Meisel*, 3:736; R. E. C. Stearns in Nautilus, 5:121–124 (portr.), 1892, and in Science, 28:243, 1908.

NORTON, ANDREA MASSENA, 1853–1930

Badè, 2:71, perhaps A. M. Norton (?); cf. J. T. Howell in Leafl. West. Bot., 2:99, 1938.

NUNENMACHER, FREDERICK WILLIAM, 1870–

Essig, 717–719 (portr.).

NUTTALL, THOMAS, 1786–1859

Alden, 42–46 (portr.); *Blankinship*, 5–6; *Brewer*, 555; *Britten*, 231; *Candolle*, 437; *DAB; Dall*, 47; *DNB; Eastwood*, 341; *Ewan*, 273; *Gray*, 1:326; *Harshberger*, 151–159, with some errors (portr.); *Hughes*, 12; *Lasegue*, 464; *Liverpool*, 55 *et passim* (portr.); *Meisel*, 1:215–216 and 3:737; *NCAB*, 8:374 (portr.); *Palmer*, 289 (portr.); *Piper*, 14–15; *Sherborn; Stone*, 7–9; F. V. Coville in Proc. Biol. Soc. Wash., 13:109–121, 1899; F. W. Pennell in Bartonia, 18:1–51, map (portrs.), 1936, the most complete and accurate acct.; W. Brewster in Mem. Nuttall Ornith. Club, 4:73–81, *et passim* (portr.), 1906; W. L. Jepson in Madroño, 2:143–147 (frontis. portr.), 1934; W. C. Coker in Elisha Mitchell Sci. Soc. Journ., 57:102–104, 1941.

OSGOOD, WILFRED HUDSON, 1875–1947

Ewan, 274; Who's Who in Amer. for 1946; C. C. Sanborn in Journ. Mammal. 29:95–112 (portr.), 1948.

OSTENSACKEN, CARL ROBERT ROMANOVICH VON DER, 1828–1906

Carpenter, 76; *DAB; Essig*, 724–727 (portr.); *Meisel*, 3:737; *Sherborn;* autobiog. Record of My Life Work in Entomology, Cambridge, Mass., 1903, pts. 1 and 2, and Heidelberg, 1904, pt. 3. Only 225 copies printed; copy no. 138 examined at John Crerar Library, Chicago; J. M. Aldrich in Entom. News, 17:269–272 (portr.), 1906; C. W. Johnson, *ibid.*, 273–275, 1906; J. B. Smith in Pop. Sci. Mo., 76:468 and 473 (portr.), 1910.

PALMER, ELIZABETH DAY, 1872–1945

T. S. Palmer, her brother, in Auk, 67:429, 1950; M. A. thesis, Univ. Calif., 1909: A taxonomic revision of the genus *Chorizanthe* R. Br. ms.

PARKER, HUBERT G., (?)–1888

Dean, 2:232; H. W. Henshaw in Condor, 22:8–9, 1920.

PARRY, CHARLES CHRISTOPHER, 1823–1890

Badè, 1:343 and 2:242–243; *Blankinship*, 8; *Brewer*, 556 and 559; *Britten*, 237; *Candolle*, 439; *DAB; Ewan*, 278; *Geiser-two*, 279; *Harshberger*, *passim; Kelly*, 180–186 (portr.); *Lemmon*, 11–12; *Meisel*, 1:217–218 and 3:737 *NCAB*, 13:228; *Sargent*, 7:130; *Stillman*, 167; *Urban Symb. Ant.* 98; M. E. Jones, Contr. West. Bot., 17:3–6, 1930; J. G. Lemmon in Pac. Rural Press, 39:385 (portr.), Apr. 12, 1890; N. L. Britton in Bull. Torrey Bot. Club, 17:74–75, 1890; *Woodcock & Stearn*, 305.

PARSONS, MARY ELIZABETH

Author of highly popular Wild Flowers of California, San Francisco, 1897.

PAULSEN, OVE

Cf. Madroño, 1:12–18 (portr.), 1916.

PEABODY, A.

Brewer, 557.

PEALE, TITIAN RAMSEY, 1799–1885

Alden, 51–52; *ACAB; Carpenter*, 78; *DAB; Ewan*, 281; *Meisel*, 1:218 and 3:738; *NCAB*, 21:170–171, portr. as "1800–1885"; *Stone*, 6–7; P. P. Calvert in Entom. News, 24:1–3 (portr.), 1913; H. H. Bartlett in Proc. Amer. Philos. Soc., 82:640–644, 1940.

PICKERING, CHARLES, 1806–1878

Alden, 49–51; *Brewer*, 555; *Carpenter*, 79; *DAB; Ewan*, 283; *Harshberger*, 190–193; *Hughes*, 15; *Kelly*, 151–153; *Meisel*, 1:219; *NCAB*, 13:176; *Piper*, 15; *Van Steenis*, 406–407; J. H. Barnhart in Mem. Torrey Club, 16:298, 1921; F. S. Collins in Rhodora, 14:57–68, 1912; W. W. Diehl in Mycologia, 13:38–41, 1921; C. S. Sargent, Sci. Papers Asa Gray, 2:406–410, 1889; F. W. Pennell in Bartonia, 21:53, 1942; H. H. Bartlett in Proc. Amer. Philos. Soc., 82:646–650, 1940.

PLUMMER, SARA ALLEN

Brewer, 558; *s.v.* J. G. Lemmon, her husband, *ante*.

PRATTEN, HENRY

Meisel, 3:640; W. C. Coker in Elisha Mitchell Sci. Soc. Journ., 57:154, 1941.

PRICE, WILLIAM WIGHTMAN, 1871–1922

Bradley Bib., 5:689; L. H. Miller, Lifelong Boyhood, 73–103, 1950; E. W. Nelson in Mem. Nat. Acad. Sci., 16:145, 1921; W. K. Fisher in Condor, 25:50–57 (portr.), 1923; relationship, if any, to forester Overton Westfeldt Price (cf. *Quercus pricei* Sudworth), not determined.

RANDALL, ANDREW

R. C. Miller in Pacific Discovery, 6(2):20, 1953.

RANSOM, LEANDER, 1800–1872

Bradley Bib., 1:210; *Brewer*, 557; W. C. Ransom, Hist. Outline of the Ransom Family of America, 1903; D. A. R. Records of the Families of Calif. Pioneers, 12:374, 376.

RATTAN, VOLNEY, 1840–1915

Brewer, 558; *Jepson*, 1:168–170 (portr.), 1928.

READY, GEORGE HENRY, 1858–1903

T. S. Palmer in Condor, 33:221, 1931.

REMY, EZECHIEL JULES, 1826–1893

ACAB; Bradley Bib., 5:716; *Embacher*, 246; *Ewan*, 288; *NBG; Wagner-three*, 364; V. MacCaughey in Hawaiian Forester and Agric., 16:26–27, 1919; assoc. in his travels with Rev. Julius Lucius Brenchley, 1817(?)–1873, English missionary; ms. Vocabulaire Havaiien-Français, 167 pp. in Ayer Coll., Newberry Library (Butler, 1768) and another ms. Vocabulaire Français-Havaiien. Recuelli dans l'Archipel de Hawaii pendant les années 1852–1855, 250 pp. (Butler, 1769).

RICH, WILLIAM

Dall, 106; *Meisel*, 3:644; *Van Steenis*, 434.

RICHTHOFEN, FERDINAND PAUL WILHELM VON, 1833–1905

Brewster; Embacher, 247; *Sherborn; Van Steenis*, 435; Bretschneider, Botanical Discoveries in China, 943, 1898; Poggendorff, Biog. Liter. Handwörterbuch, 3:1121, 1898, and 5:1048, 1926.

RICKSECKER, LUCIUS EDGAR, 1841–1913

Carpenter, 85; *Ewan*, 289; *Essig*, 738–741 (portr.); H. C. Fall in Entom. News, 24:239–240, 1913.

RITTER, WILLIAM EMERSON, 1856–1944

Amsci, ed. 7; *Dean*, 2:350; T. S. Palmer in Auk, 64:665–666, 1947; F. B. Sumner Life History of an American Naturalist, 198–209, *et passim*, 1945; L. H. Miller, Lifelong Boyhood, 28–32, 104, *et passim*, 1950; D. S. Jordan, Days of a Man, 1:541, 1922; autobiog. notes in California Woodpecker and I, 315–318, *et passim* (portr.), Berkeley, Calif., 1938.

RIVERS, JAMES JOHN, 1824–1913

Carpenter, 86; *Essig*, 746–747 (portr.); *Sherborn; Ewan*, 290.

RIXFORD, EMMET, 1865–1938

Amsci. ed. 5; anon. in Nautilus, 51:141, 1938.

RIXFORD, GULIAN PICKERING, 1838–1930

Amsci, ed. 4; *NCAB*, Vol. B:172 (portr.) and 35:537–538 (portr.); W. C. Tesche in Journ. Heredity, 21:98–106 (portr.), 1930; Millspaugh and Nuttall, Field Mus. Nat. Hist. Publ. Bot., 5:33, 1923.

ROEZL, BENEDICT, 1823–1885

Bradley Bib., 5:734; *Ewan*, 291; *Woodcock & Stearn*, 231, 302; S. B. Parish in Bot. Gaz., 44:414, 1907, and 48:462–463, 1909; autobiog. in Gard. Chron., ser. 2, 2:73 (portr.), 1874, reprinted, *ibid.*, ser. 2, 24:521–522 (portr.), 1885; E. Regel in Gartenflora, 21:369, 1872, and 34:330–331, 1885; E. Morren in Belg. Hort., 30:5–12 (portr.), 1880; A. Eastwood in Leafl. West. Bot., 5:103, 1948.

ROSE, LEWIS S.

J. T. Howell in Leafl. West. Bot., 7:91, 1953.

RÜBEL, EDUARD AUGUST, 1876–

Cf. Madroño, 1:12–18 (portr.), 1916.

SAMUELS, EMANUEL, 1816–1886

Palmer, 294 (portr.); H. W. Henshaw in Condor, 21:106–107, 1919.

SAXE, ARTHUR WELLESLEY, 1820–1891

Dean, 2:396, where no initials given; *Kelly*, 178–179 (portr.).

SCAMMON, CHARLES MELLVILLE

Dean, 2:396.

SCHRÖTER, CARL JOSEPH, 1855–1939

Cf. Madroño, 1:12–18 (portr.), 1916; *Van Steenis*, 476–477 (portr.).

SEEMANN, BERTHOLD CARL, 1825–1871

Britten, 271; *DNB; Embacher*, 267; *Hulten*, 300; *Van Steenis*, 481.

SESSIONS, KATE OLIVIA, 1857–1940

Bradley Bib., 5:795; T. D. A. Cockerell in Bios, 14:167–179 (portrs.), 1943; cf. L. H. Bailey in Gentes Herbarum, 4:99–105 (portr.), 1937.

SETCHELL, WILLIAM ALBERT, 1864–1943

Amsci. ed. 6; T. H. Goodspeed in Essays in Geobotany. In Honor of William Albert Setchell, xi–xxv (frontis. portr.), 1936; L. Constance in Journ. Wash. Acad. Sci., 33:288, 1943; H. L. Mason in Madroño, 7:91–93 (portr.), 1943; C. R. Ball, *ibid.*, 5:231–232 (portr.), 1940; D. H. Campbell in Nat. Acad. Sci. Biog. Mem., 23:127–147 (portr.), 1945.

SILLERN, WILLIAM

Cf. G. R. Agassiz, Letters and Recollections of Alexander Agassiz, 161, 1913.

SIMPSON, GEORGE, –1860

Embacher, 271 *s.v.* Thomas Simpson; *Stillman*, 325; *Wagner-three*, 140; A. S. Morton, A History of the Canadian West to 1870–71, *passim*, n.d.

SINCLAIR, ANDREW, 1796–1861

Britten, 276; *DNB; Van Steenis*, 485; Rewa Glenn, Botanical Explorers of New Zealand, 107–114, 1950; H. F. von Haast, Life and Times of Sir Julius von Haast, 173 *et passim*, 1948.

SKOTTSBERG, CARL JOHAN FREDRIK, 1880–

Cf. Madroño, 1:12–18 (portr.), 1916; *Van Steenis*, 486–487.

SLEVIN, JOSEPH RICHARD, 1881–

[Calif.] Academy News Letter no. 164 (portr.), 1953; E. W. Nelson in Mem. Nat. Acad. Sci., 16:144, 1921; I. M. Johnston in Proc. Calif. Acad. Sci., ser. 4, 20:13, 1931.

SLEVIN, THOMAS EDWARDS, 1871–1902

Palmer, 296; L. M. L(oomis) in Auk, 20:326–327, 1903.

SLOAT, LEWIS W.

R. C. Miller in Calif. Hist. Soc. Quart., 21:364, 1942, and Pacific Discovery, 6(2):18–25, 1953; evidently Sloat's dupls. did not reach the National Museum *teste* H. A. Rehder, who checked the records for me there.

SMITH, CHARLES PIPER, 1877–

Cf. Madroño, 4:283, 1938; *Ewan*, 306.

SNODGRASS, ROBERT EVANS

Dean, 2:465–466; D. S. Jordan, Days of a Man, 1:577, 1922.

SNYDER, JOHN OTTERBEIN, 1867–

Dean, 2:466; D. S. Jordan, Days of a Man, *passim*, 1922.

SONNE, CHARLES FREDERICK, 1845–1913

Badè, 2:308; *Jepson*, 2:115–116 (portr.), 1934.

STARKS, EDWIN CHAPIN, 1867–1932

Amsci, ed. 4; *Dean*, 2:478–480; W. M. Mann, Ant Hill Odyssey, 64–71, 1948.

STEARNS, ROBERT EDWARD CARTER, 1827–1909

Bradley Bib., 5:821; *Dean*, 2:481; W. H. Dall in Science, 30:279–280, 1909; Mary R.

Stearns in Smithson. Misc. Coll., 56(18):1–15, 1912, bibliog. (portr.); H. W. Henshaw in Condor, 21:107, 1919; autobiog. notes in Amer. Nat., 13:141–154, 1879.

STILLMAN, JACOB DAVIS BABCOCK, 1819–1888

Brewer, 556; J. D. B. Stillman, "Old Fuller," Overland Mo., 14:557–559, June, 1875; ms. notes in Ewan files; cf. Calif. Med. Gazette, 2:152–153, 1870, for unsigned edit. concerning the work of the State Geol. Survey.

STEWART, ALBAN, 1875–1940

Amsci, ed. 6.

STIVERS, CHARLES AUSTIN

Jepson, 2:28 (portr.), 1931.

STOMPS, THEODOOR JAN, 1885–

Cf. Madroño 1:12–18 (portr.), 1916; *Van Steenis*, 508–509 (portr.).

STOUT, ARTHUR B.

Though initial is generally given as "B" the physician who was one of the original members of the Academy may be "A. A. Stout, M.D., U.S.N.," elected to the New York Academy (Lyceum of Nat. Hist.) in 1847.

STREET, JOSEPH A.

Cf. A. Eastwood in Occ. Pap. Calif. Acad. Sci., 9:3, 1905.

STRETCH, RICHARD HARPER, 1837–1923

Carpenter, 101; *Essig*, 767–770 (portr.), who cites 1926 as death year; K. R. Coolidge and H. H. Newcomb in Entom. News, 31:181–185 (portr.), 1920.

SUMNER, FRANCIS BERTODY, 1874–1945

Dean, 2:517–518; *NCAB*, 34:333–334 (portr.); R. R. Heustis in Journ. Mammal., 27:1–3 (portr.), 1946; C. M. Child in Nat. Acad. Sci. Biog. Mem., 25:147–173 (portr.), 1949; autobiog, Life History of an American Naturalist, 1945.

SWARTH, HARRY SCHELWALDT, 1878–1935

Amsci, ed. 5; *Palmer*, 298; J. Mailliard in Auk, 54:127–134 (portr.), 1937; J. M. Linsdale in Condor, 38:155–168 (portr.), 1936.

TANSLEY, ARTHUR GEORGE, 1871–

Cf. Madroño, 1:12–18 (portr.), 1916.

TAYLOR, HENRY REED

H. Harris in Condor, 43:51, 1941; cf. Pac. Coast Avifauna, 5:153, 1909, for his papers.

THOUARS, ABEL AUBERT DU PETIT, 1793–1864

Lasegue, 385–386; cf. J. T. Howell in Leafl. West. Bot., 1:189–191, 1935; J. Espasa, Enciclopedia Univ. Ilustrada; C. Nissen, Bot. Buchillustration, 2:54, 1951.

TIDESTROM, IVAR, 1865–

Amsci; Ewan, 321; *Rydberg*, 45; M. E. Jones, Contr. West. Bot., 15:20–24, 1929; autobiog. notes in I. Tidestrom and Sister T. Kittell, Flora of Arizona and New Mexico, ix–x, 1941.

TILING, HEINRICH SYLVESTER THEODOR, (?)–1871

Hultén, 301; cf. *Bradley Bib.*, 1:455 for Florula ajanensis, in collaboration with E. Regel. Regel described *Horkelia tilingi* and *Mimulus tilingi* from his collections taken in vicinity of Nevada City.

TORREY, HARRY BEAL, 1873–

Amsci; cf. H. Kirby in Sci. Mo., 61:416, 1945.

TORREY, JOHN, 1796–1873

Brewer, 558; *DAB; Ewan*, 322; *Kelly*, 136–144; *Meisel*, 1:234 and 3:666–667; *Rodgers' Torrey, passim;* Torrey's visit to the Academy seems not to have been chronicled.

TOWNSEND, CHARLES HASKINS, 1859–1944

Dean, 2:549–550; *Hulten*, 306; *NCAB*, 32:37 (portr.); *Palmer*, 298; T. S. Palmer in Auk, 64:349–350, 1947; D. S. Jordan, Days of a Man, *passim*, 1922; autobiog. in Condor, 29:224–232 (portr.), 1927.

TOWNSEND, JOHN KIRK, 1809–1851

Alden, 40–42; *DAB; Dall*, 41 *et passim; Dean*, 2:550; *Ewan*, 323; *Meisel*, 1:235; *Palmer*, 299; *Stone*, 7–11; *Wagner-three*, 79; W. Stone in Cassinia, 7:1–5 (portr.), 1903; F. W. Pennell in Bartonia, no. 18, 35, *et passim*, 1936; H. Harris in Condor, 43:21–23, 1941; cf. Stone in Auk, 47:414–415, 1930; cf. J. Grinnell in Univ. Calif. Publ. Zool., 38:269–270, 1932; though Townsend is intimately associated with California natural history he did not visit the State.

TRASK, JOHN BOARDMAN, 1824–1879

Jepson, 2:117–118, 1924; *Meisel*, 1:235; A. W. Vodges in Trans. San Diego Soc. Nat. Hist., 1:27–30, 1907; R. E. C. Stearns in Science, 28:240–243, 1908.

TROWBRIDGE, WILLIAM PETIT, 1828–1892

DAB; Dall, 299; *Palmer*, 300; C. B. Comstock in Nat. Acad. Sci. Biog. Mem., 3:363–367, 1895.

TSCHERNIKH, GEORGE, fl. 1835–1841

Essig, 772–773.

TUBEUF, KARL VON

Cf. Madroño, 1:12–18 (portr.), 1916.

VANCOUVER, GEORGE, 1758–1798

Brewer, 553; *DNB; Eastwood*, 336; E. S. Meany, Vancouver's Discovery of Puget Sound, 7–21, *et passim* (portr.), 1915; Geo. Godwin, Vancouver: a Life, 1758–1798, 1930.

VAN DENBURGH, JOHN, 1872–1924

Amsci, ed. 3; edit. note in Condor, 27:83, 1925; D. S. Jordan, Days of a Man, 1:541 and 710, 1922.

VAN DUZEE, EDWARD PAYSON, 1861–1940

Amsci, ed. 6; H. Osborn, Fragments of Entom. Hist., 1:234 (portr., pl. 5), 1937.

VAN DYKE, EDWIN COOPER, 1869–

Amsci; Hultén, 323; H. Osborn, Fragments of Entom. Hist., 1:284 (portr., pl. 28), 1937; W. M. Mann, Ant Hill Odyssey, 79–80, 1948.

VASEY, GEORGE RICHARD

Brewer, 559; *Ewan*, 327; *Harshberger*, 385; *Piper*, 18; cf. J. T. Howell in Amer. Midl. Nat., 30:33–35, 1943.

VEATCH, JOHN ALLEN, 1808–1870

Bradley Bib., 5:876; *Geiser-two*, 282; cf. mimeo. letter addressed to W. P. Webb, ed., Southwestern Hist. Quart., dated 18 Sept., 1942, circularized by S. W. Geiser, relating to Veatch's genealogy; P. A. Munz in Leafl. West. Bot., 7:70, 1953; cf. Amer. Journ. Sci., ser. 2, 26:288–295, 1858, for Veatch's account of mud volcanoes of Salton Sea; Hesperian, 2:21–26, 1859, for his account of Clear Lake, Calif., and *ibid.*, 3:529–534, 1860, for his account of Cerros (i.e., Cedros) Island.

VOLLMER, ALBERT MICHAEL

Woodcock & Stearn, 361.

Vosnesensky, Ilya Gavriloch, 1816–1871

Brewer, 555, as "Wosnessensky"; *Eastwood*, 338; *Essig*, 777–789 (portr.); *Hultén*, 300; cf. J. Grinnell in Univ. Calif. Publ. Zool., 38:321, 1932.

Vries, Hugo de, 1848–1935

A. D. Rogers, III, Liberty Hyde Bailey, *passim*, 1949; E. Nordenskiöld, Hist. Biol. (A. Knopf, ed.), 587–588, 1928, and other general histories of science; portr. in Chron. Bot., 9(5–6), pl. 22, 1946, at Burbank's garden: autobiog. notes in Naar Californie, Amsterdam, 1905, and transl. in Pop. Sci. Mo., 67:329–347, 1905.

Wallace, Alfred Russel, 1823–1913

Britten, 314; *Carpenter*, 109; *Dean*, 2:599–600; *DNB*, 20th Cent. Suppl. 546; *Ewan*, 330; *Musgrave*, 337; *Urban Fl. Bras.*, 130–131; *Van Steenis*, 555–557; L. O. Howard, Fighting the Insects, 303–305, 1933; W. S(tone) in Auk, 31:138–141, 1914; D. S. Jordan. Days of a Man, 1:303, 1922; T. D. A. Cockerell in Pop. Sci. Mo., 62:517–518, 1903.

Walther, Eric

V. Reiter, Jr., in Leafl. West. Bot., 7:82–83, 1953.

Webber, David Gould, 1809–(?)

J. Ewan in A. S. Hitchcock, Man. Grasses U. S., ed. 2 (U.S.Dept. Agri. Misc. Publ. 200), 989, 1951.

Webber, Herbert John, 1865–1946

Fairchild, 444, *et passim*, and World Grows round my Door, *passim*, 1947; H. S. Reed in Madroño, 8:193–195, 1946, portr. as frontis. to Vol. 8.

Whipple, Amiel Weeks, 1816–1863

DAB; Howell, 30; *Ewan*, 335; G. Foreman, A Pathfinder in the Southwest, Norman, Okla., 1941.

Whitney, Josiah Dwight, 1819–1896

ACAB; Badè, *passim; Brewster*, 206–207, 239–240, 272–273, *et passim; DAB; Ewan*, 336; *Meisel*, 1:239; *Palmer*, 302; brief acct. of Calif. Geol. Surv. in No. Amer. Rev., 121:63–64, 1875.

Wickson, Edward James, 1848–1923

DAB; Fairchild, 302; W. L. Howard in Chron. Bot., 9:314–316, *et passim* (portr., pl. 22), 1946.

Wilkes, Charles, 1798–1877

Brewer, 551; *DAB; Dall*, 71–72, *et passim; Ewan*, 337; *Hughes*, 15; *Meisel*, 1:240 and 3:678; *Urban Fl. Bras.*, 1:144–145; *Van Steenis*, 575–577; J. D. Hill, Sea Dogs of the Sixties, 88–127 (portr.), 1935; H. H. Bartlett in Proc. Amer. Philos. Soc., 82:601–705, 1940; M. E. Cooley, *ibid.*, 82:707–719, 1940.

Williams, Francis Xavier, 1882–

Amsci; Musgrave, 354; portr. in Pacific Discovery, 6(2):22, 1953.

Williamson, Robert Stockton, 1824–1882

Hume, 195, *et passim; Palmer*, 303.

Wislizenus, Frederich Adolph, 1810–1889

Brewer, 557; *Dall*, 180, 258, 265; *Ewan*, 338; *Geiser-two*, 283; *Meisel*, 1:242 and 3.680; *Sargent*, 6:94; *Wagner-three*, 83; Geo. J. Engelmann in St. Louis Acad. Sci. Trans., 5:464–468, 1892; F. Starr in Pop. Sci. Mo., 52:643–644 (portr.), 1898; P. Spaulding, *ibid.*, 74:244–246 (portr.), 1909; biog. sketch by his son in Mo. Hist. Soc. ed. of W's Journey, 5–13 (portr.), 1912.

Wistar, Isaac Jones, 1827–1905

NCAB, 12:359 (portr.); see Autobiography, Phila. 1914, reissued in 1937 and again in 1938.

WOOD, ALPHONSO, 1810–1881

ACAB; Brewer, 558; *Meisel*, 1:242; *NCAB*, 14:278; O. R. Willis, A Biographical Sketch of Dr. Alphonso Wood, of West Farms . . ., 6 pp. (n.d.), examined in N. Y. Bot. Gard. Library; anon. in New York [Times?] for April 19, 1903 (portr.); C. J. Lyon in Dartmouth Alumni Mag., 31:18, 81–82, March, 1939, and in Science, 101:484–486, May 11, 1945; *Woodcock & Stearn*, 364.

WOODHOUSE, SAMUEL WASHINGTON, 1821–1904

Ewan, 340; *Geiser-two*, 283; *Hume*, 469–509 (portr.), the fullest act.; *Palmer*, 303; *Sargent*, 8:88; *Wagner-three*. 230; W. Stone in Cassinia, 8:1–5 (portr.), 1904; W. S(tone) in Auk, 22:104–106, 1905.

WOODWORTH, CHARLES WILLIAM, 1865–1940

Carpenter, 114; *Essig*, 800–802 (portr.).

WRANGELL, FERDINAND PETROVICH, 1794–1870

Brewer, 554, as Wrangel; *Embacher*. 299, as "1795–1870"; *Essig*, 802; *Hultén*, 300.

WRIGHT, CHARLES, 1811–1885

Brewer, 558; *DAB; Ewan*, 342; *Geiser-two*, 283; *Urban Symb. Ant.*, 141; C. S. Sargent, Sci. Pap. of Asa Gray, 2:468–474, 1889.

WRIGHT, WILLIAM GREENWOOD, ca. 1830–1912

Carpenter, 115; *Essig*, 802–804 (portr.); *Hultén*, 308; J. D. Gunder in Entom. News, 40:33–34 (portr.), 1929; F. Grinnell, Jr., in Entom. News, 24:91–92, 1913, and Bull. So. Calif. Acad. Sci., 12:19–21, 1913; his Butterflies of the West Coast, San Francisco, 1905, is a rare book from the destruction of the stock in the 1906 fire.

XANTUS DE VESEY, LOUIS JOHN, 1825–1894

Brewer, 558; *Embacher*. 300; *Essig*, 804–808, map; *Geiser-two*, 283, *s.v.* "Württemberg"; *Hume*, 510–532 (portrs.), useful acct.; *Meisel*, 1:244 and 3:743; *Palmer*, 304; *Wagner-three*, 316; Henry M. Madden, Xantus, Hungarian Naturalist in the Pioneer West, Palo Alto, 1949, the latest full-length biog.; J. Grinnell, J. S. Dixon, and J. M. Linsdale, Fur-bearing Mammals of California, 1:76–77, 1937.

A CENTURY OF ASTRONOMY AND GEODESY IN CALIFORNIA

By ERWIN G. GUDDE
University of California

UNTIL 1769 California remained a geographical conception. Navigators—with the exception of Francis Drake, all Spanish or in Spanish service—had sailed up and down the coast, but they had come, not for scientific observation, but in search of fabulous rich lands, of booty on the high sea, of harbors in which the Manila galleon could find safety. Their observations of latitude and longitude were completely inadequate and caused cartographers for two centuries to indulge in imaginary geography of the somewhat mythical land, "California."

In 1769 the land route to California was opened up by the Portola expedition and during the next half-century the Spaniards made California into a Spanish colony. The representatives of Spanish imperialism who created the new province were the officers of the military detachments and the Franciscan fathers. There were among the latter some personalities—Crespi, Garcés, Palou—who left their mark upon California history because in the vastness and newness of the territory they were the only ones who could read, write, and observe. They lacked, however, the scientific fervor which, in addition to the religious fervor, had distinguished their predecessors on the American continent—the Jesuits. Hence the few astronomical and geodetic data left by these *padres* are negligible and unimportant. After California became a Mexican province and until the occupation by the United States not even a trace of scientific activity existed in California.

Whatever scientific work was done before United States scientists began their task was accomplished, not by the Spaniards or Mexicans, but by the foreign navigators and explorers: La Pérouse, Vancouver, Kotzebue, Belcher, Beechey, Wilkes, Frémont. Indeed, Beechey's geodetic and hydrographic work of San Francisco Bay was so accurate that the United States Coast Survey, when it started its work in 1850, allowed the resurvey of the harbor to wait and undertook other tasks which seemed more pressing.

Real astronomic and geodetic work began with the end of the Mexican War. It was mainly army engineers who began the great task of establishing the boundaries, surveying the land, and examining and evaluating its resources and possibilities. Greatly accelerated was the progress of these tasks when California suddenly moved into the center of world interest after the discovery of gold. Next to gold-seekers, traders, and lawyers (who reaped a rich harvest in connection with the disposal of the land grants), the engineers formed the largest contingent of professions that descended upon California. The coast had to be made safe for navigation, base lines had to be established, land grants measured, transportation established, minerals assayed, resources investigated—tasks for every type of engineering. All scientific knowledge available at that time was used for practical purposes. Science for science's sake was unknown in those hectic years following the Gold Rush. Astronomy played a role only in so far as the elements of the science were essential to the geodetic work necessary to create the basis for material culture.

In 1848 the United States Coast Survey, one of the most efficient Federal agencies, then under the direction of Alexander Bache, Benjamin Franklin's grandson, decided to start the survey of the Pacific Coast in the following year. A hydrographic and a geodetic party, both well equipped, arrived in California in 1849. Both came to naught; the lure of the goldfields proved to be too strong for the underpaid employees of the Government.

In 1850 George Davidson and a group of stalwart young members of the Coast Survey arrived in San Francisco. They had volunteered to go to the Pacific Coast out of cheerful, youthful exuberance. For almost half a century Davidson was one of the leading figures in the evolution of the State. In the development of the sciences of astronomy, geodesy, geography, and seismology in California he dominated the scene. The Coast and Geodetic Survey, the California Academy of Sciences, and the University of California owe much to this indefatigable, universalistic, and, above all, practical scientist.

The auguries, to be sure, were not very encouraging. The journey of the four young geodesists—Lawson, Harrison, Rockwell, and Davidson—consumed one-fourth of the year's allotment for the Pacific Coast work. In San Francisco they soon realized that their salary of $800 per annum would not last very long if they had to pay $7.50 for room and board per diem. They had to bivouac with their 2,500 pounds of instruments in a 12 by 12-foot room. The water for ablution and for washing their shirts they carried from a spring four blocks away. The only mechanic in the city charged them $900 for making four large foot screws and for tapping the cast-iron frame of the large transit instrument.

Davidson resisted the temptation to start the survey of the Golden Gate and San Francisco Bay. He realized that Beechey's survey was good and that other points along the coast needed urgent attention. The islands of the Santa Barbara Channel were badly located, the position of Point Conception was in error, and thither the party embarked the end of June, 1850. There, at El Cojo, the real hardships began. The Mexican cook promptly absconded with their horse and the party had to cook their steaks and flapjacks over a fireplace made of three whale vertebrae and fed by dry cattle chips, and to do all other chores necessary to maintain the most primitive essentials of human existence.

But the work was done. Three months and a half were spent in astronomical observations for the latitude and longitude of the station. The observations included lunar transits, occultations of stars by the moon, and one solar eclipse. In spite of the fog, Davidson could observe for sixty nights until he was "heartily sick of starlight." Returning to San Francisco in October, the party worked systematically on the reductions of the field observations. Their preliminary work proved so satisfactory to the Superintendent of the Survey that he procured an extra appropriation for the party. Assistants and laborers could be hired and the work at the second station, Point Pinos, could be carried on under more agreeable circumstances during January and February, 1851.

As the third station, Davidson selected San Diego, because its latitude on the existing charts was completely erroneous.

At this port [he wrote], I made the usual astronomical observations of lunar transits, occultations of stars by the moon, latitude observations, azimuth observations for the triangulation, determination of the magnetic elements, etc., working the greater part of the night and computing the greater part of the day. I had undertaken work on this coast to make a record in a new field, and therefore labored nearly to the utmost strain of my energies, never less than eighteen hours a day.

After this first year of astronomic observation and determination the work of the United States Coast Survey was carried on with ever-increasing speed, volume, and variety. Until his retirement in 1895, except for the years during and after the Civil War, which were spent chiefly in war work at Philadelphia, Davidson was in charge of the astronomic, geodetic, topographic, and hydrographic work of the Pacific Coast and later also of the coast of Alaska.

Besides the practical work the members of the Coast Survey inaugurated astronomical observation on the Pacific Coast. While at Monterey Bay in the winter of 1850–1851, Davidson began his computation of the star factor tables, which were later published. In 1852 he discovered and observed a brilliant comet at Astoria on the Columbia River. The solar eclipse of May 26, 1854, was observed by members of the Survey at Benicia, Loma Prieta, and Humboldt Bay. Davidson also observed the solar eclipse of March 25, 1857, in San Francisco. In 1856 he published the "Occultation of Stars by the Moon on Western Coast of the United States," and in the following year "The Occultation of 22 Stars of the Pleiades, and Solar Eclipse of 1857."

The crowning achievement of Davidson during his first phase of Pacific Coast Survey was a practical work, the *Directory of the Pacific Coast,* first published in 1857. This work, republished at irregular intervals and later called *Coast Pilot of California, Oregon and Washington,* systematized the astronomic, geodetic, hydrographic, and topographic work of the Coast Survey and became the bible of the mariners who sailed up and down the Pacific Coast.

The year in which Davidson left San Francisco, 1860, witnessed the first attempts of astronomical observations by agencies other than the United States Government. To the University of Santa Clara belongs the honor of being the first educational institution of the State to acquire a telescope. The 4-inch refractor with altazimuth mounting, installed in 1860, was the nucleus of an observatory which in later years became well known, especially through Jerome Ricard's observations of sun spots and faculae.

In the same year an amateur astronomer, George Madeira, started observing with a 3-inch refracting telescope with equatorial mounting at Volcano, Amador County. According to Campbell, on June 30, 1861, Madeira discovered the brilliant Comet 1861 II only a few hours after its discovery in Europe.

In the meantime other agencies were at work surveying the State. A United States Commissioner of the General Land Office was sent to California shortly after the treaty of Guadalupe Hidalgo had been signed. The principal tasks of his office were the establishment of the extent of the Spanish and Mexican land grants and the division of the newly acquired territory into townships. The commissioner established the three township base lines and meridians: the Mount Diablo, the San Bernardino, and the Humboldt, which have formed the skeleton for land-measuring purposes ever since. While the Land Office did extremely valuable work for the future development of the State, unlike the Coast Survey it did not contribute to the advancement of astronomy and scientific geodesy.

Another Federal project consisted of the explorations and surveys to ascertain the most practical route for a railroad from the Mississippi to the Pacific, undertaken in 1853–1854 under the direction of the United States War Department. The result of this well-equipped project was published in a *Report* of thirteen imposing volumes—a great contribution to the geography and cartography as well as to the natural conditions and resources of the American West. At no less than 174 stations, including many in California, astronomical observations were made and the latitude, longitude, and magnetic declinations of many places were determined. The tables of these observations were published in the second volume of the *Report* and formed a valuable basis for future surveys, especially for the heretofore neglected mountainous and desert regions of the State.

The government of the State likewise participated in the geodetic delineation of California. The office of Surveyor General of the State of California, founded in 1850, published annual reports. In 1860 the legislature established the State Geological Survey, which carried on its tasks for fourteen years until a new political constellation put a sudden end to its work, so that not even its valuable maps could be completed. The principal work was carried on by four great men in the fields of geodesy, geology, and topography, Josiah D. Whitney, Clarence King, Charles F. Hoffmann, William H. Brewer.

The work of the Coast Survey continued, and its annual reports bear witness to the excellent achievements of its members. It received a new impetus when in 1868 Davidson was again put in charge of the survey on the Pacific Coast, an assignment which he continued uninterruptedly until 1895.

During the eight years of absence from San Francisco, Davidson had achieved national recognition. He had participated in the War between the States in various capacities, had been the engineer of a party sent to Panama to examine the possibility of a canal through the isthmus, and had been sent to Alaska by the State Department to make a survey of the territory preliminary to the consummation of its purchase by the United States.

With renewed vigor Davidson took up his various tasks. Soon after his return he became intimately connected with two California institutions to which he remained devoted till the end of his life: the University of California and the California Academy of Sciences. In 1870 he was elected Professor of Astronomy and Geodesy, in 1877 he became a Regent of the University, and after his retirement from the Coast Survey he was appointed Professor of Geography; a year before his death he received the degree of Doctor of Laws.

His first contribution to the *Proceedings of the California Academy of Sciences* was a report on the "Observations of the Meteors of November 14, 1869, at Santa Barbara." In the course of years he contributed about thirty papers on astronomy and geodesy alone to the periodical publications of the Academy. In 1872 he was elected President of the Academy, an office which he held for fifteen years.

In his capacity as President he visited James Lick to convey the thanks of the institution for a most munificent endowment, the valuable corner lot of Fourth and Market Streets, which Lick had deeded to the Academy on February 15, 1873.

Of the many strange characters who had come to California in the early days, James Lick was perhaps the most peculiar. Whereas thousands rushed to California to make a fortune, Lick arrived in the early part of 1848 bringing with him a handsome capital, acquired through twenty years of hard work as a cabinet- and piano-maker in South America. In another twenty years he greatly increased this fortune and decided to spend it for the benefit of his adopted state and for the glorification of his name.

Upon Lick's request Davidson repeated his visits and was finally let in on a secret: Lick wanted to create a new world wonder by erecting a telescope much larger and much more powerful than any in existence. The somewhat conservative Davidson soon realized that Lick had strange ideas about such a telescope, that he expected that it would provide spectacular discoveries in the universe, and that it would be a world-wide attraction. Davidson's first task was to guide Lick's enthusiasm in the right direction. He did this with tact and understanding. If in the end he did not succeed entirely, it was not his fault.

Before the location of the observatory was discussed by the cautious Davidson, a mutual friend, Dr. Frederick Zeile, the pioneer of the bathtub in San Francisco, informed him that Lick had made up his mind to build the observatory at Fourth and Market Streets in San Francisco, between the sites he had given to the Academy of Sciences and the Pioneer Society. In front of the observatory he planned to erect three statues: one for Francis Scott Key (the one now standing in front of the Academy of Science buildings in the Golden Gate Park), one for Thomas Paine, the pioneer of atheistic thought in America, and one for Lick's own grandfather, who had once shared the trials of Washington's revolutionary army in Valley Forge. It took Davidson several months of diplomatic and persistent argument to convince Lick that, though downtown San Francisco would doubtless be the ideal spot to attract tourists to his spectacular show piece, it left much to be desired as a site for scientific research in astronomy. Gradually he guided Lick's judgment to place the observatory in the Sierra Nevada—not on one of the high peaks where conflicting upper air currents would be detrimental to astronomical observation but near the summit of Donner Pass.

On October 20, 1873, Davidson announced at the monthly meeting of the Academy that Lick had agreed to his proposals and to the erection of an observatory with "a telescope superior to and more powerful than any telescope yet made." The next morning the *Alta Californian,* in a three-column spread on the front page, imparted the news to the world. Since the announcement of the discovery of gold no more exciting intelligence had come from California, and the names of Lick and Davidson were as much in the mouth of the people as the names of Sutter and Marshall had been twenty-five years before. The young state, which many still associated with lawlessness, fraudulent land grants, and unscrupulous lawyers, was suddenly to take the lead in the study of an important field of human knowledge.

Davidson's task, however, was not yet done. Next he had to dissuade Lick from building a reflector telescope. This type of telescope, an invention of Isaac Newton, had just then been greatly improved and was especially favored in England. Davidson, however, as well as the majority of American astronomers, considered the refractor type superior. When we realize the marvelous results obtained by reflector telescopes at the Lick, Mount Wilson, and Palomar observatories we have to admit that James Lick, the half-educated Pennsylvania-Dutch piano-maker, had the right instinctive vision and that Davidson and the other American astronomers were wrong in their conviction that a refractor of limited size would be superior to the immense reflector Lick had proposed.

After the latter had agreed to a refractor telescope he wanted one six feet in diameter, and Davidson had to convince him that a 40-inch objective would be the maximum possible size of a refractor. The question of the amount of money necessary caused more difficulties, because Lick could not see that an observatory needed other equipment besides a giant telescope. He believed that Davidson's figure of $1,500,000 was too high but finally agreed to spend $1,200,000 on the project.

In May, 1874, Davidson went East to confer with astronomers about the preparations for the observation of the transit of Venus in December. During his absence other influences gained the confidence of Lick, who decided to build the observatory on the shores of Lake Tahoe, where the name Observation Point still marks the chosen site. (As it turned out, Lick's advisor owned a quarter-section of land adjacent to the Point.) Davidson succeeded in convincing Lick of the unsuitability of this site but his patience was by this time rather taxed by the donor's constant vacillations. He made no further attempts to influence Lick when the latter cut down the endowment to $700,000 and chose Mount Hamilton, 4,209 feet elevation, as the site for the observatory. Mount Hamilton, named in 1861 for an Oakland independent clergyman, the Reverend Laurentine Hamilton, was, according to some astronomers, much better suited than Davidson's favorite spot near Donner Pass.

The work on the observatory could not begin until the Lick estate was liquidated in 1879. In 1888 the great project was completed and was given to the University of California, as provided by Lick in his final deed of trust. The 36-inch equatorial refractor was at that time the largest in the world and the general equipment of the observatory was second to none. Within a few years the fifth satellite of Jupiter, the revolving sun of the Procyon, and a large number of comets and double stars were discovered. For the first time the angular diameter of a fixed star was measured and epoch-making work was done by spectroscopic observation of stars, nebulae, and comets. This is not the place to attempt to enumerate the achievements of the distinguished astronomers connected with the Lick Observatory. Its various periodical publications give the record.

There is no question that the project of an observatory of the size and equipment of the Lick Observatory was a healthy stimulus to astronomical interest in the world. In California itself observatories began to mushroom even before the Lick Observatory was completed.

The first scientifically constructed observatory was erected by George Davidson in San Francisco for special study of the physical features of the planets, and later for observing the variations of latitude and determining the constant of aberration. Davidson had made astronomical observations on Washington Plaza since 1870. In 1879 he removed his station to Lafayette Square, equipping it with a 6.4 Clark refractor, a chronograph, and a telegraphic apparatus. Here

Davidson often observed until the small hours in the morning, and that after his strenuous duties with the Coast Survey.

> As a labor of love [says Campbell], Professor Davidson undertook the observations of latitude pairs of stars at his observatory. Between May, 1891, and August, 1892, he secured for this purpose, 5.308 observations on 283 stars. . . . His results were in good agreement with those obtained at European, Atlantic coast, and Hawaiian stations.

The results of his observations he published in numerous articles in the publications of the California Academy of Sciences, the Royal Astronomical Society, and the United States Coast Survey. The observatory remained on Lafayette Square until 1902. Its principal instrument is now at Chabot Observatory.

The sudden interest in astronomy naturally also had great influence upon astronomy as a subject of instruction in our schools. Davidson himself again took the lead by inviting high school students and their teachers to his observatory, and thus he aroused in the young intellects an interest in the wonders of the universe. In 1883 Anthony Chabot presented to the Oakland School Department his well-known observatory with an 8-inch refractor, to which the Board of Education added in 1913 a 20-inch refractor. In 1885 the College of the Pacific received an observatory with a 6-inch Clark equatorial. The Students' Observatory of the University of California was erected in 1886, and in 1892 was placed in charge of Armin O. Leuschner. It has since been the elementary training ground for many astronomers who have achieved fame in their profession. Only a year later Mills College received its observatory with a 5-inch refractor and an 8-inch reflector, and in 1890 Napa College started its astronomy department with an 8-inch Clark-Saegmuller refractor, which was later acquired by the University of Santa Clara.

However, the hopes of the University of Southern California to outdo the Lick Observatory by having an observatory with a 40-inch refractor telescope were shattered. The donor died shortly after the discs were given and insufficient funds prevented the University from erecting the observatory. The discs were purchased in 1893 by C. T. Yerkes and became the nucleus of the famous observatory of the University of Chicago! The chief factor in this move was no other than George Ellery Hale, destined to play a most important role in the development of astronomy in California. Since then astronomy has become a subject generally taught, and most colleges and many high schools have their own observatories.

George Davidson continued to play an important role in the geodetic work of the State, as in the field of astronomy. Between 1875 and 1879 Captain George M. Wheeler, Corps of Engineers, United States Army, had carried on the "Geographical Surveys West of the One Hundredth Meridian." On March 3, 1879, the United States Geological Survey was established under the Department of the Interior and began its great work of creating the topographical atlas of the United States. Important as were the Wheeler Survey and the Geological Survey —and later the United States Forestry Survey and the United States Corps of Engineers—for the scientific delineation of California, the extension of the scope of the Coast Survey was of much greater value in the line of applied astronomy. The Coast Survey, heretofore responsible for the survey of our coasts, was assigned in 1879 the tremendous task of the trigonometrical survey of the United States.

Davidson, who was, so to speak, at the western end of the arc of the 39th parallel, which extends 2,825 miles from the Atlantic Coast, entered upon his new duties with renewed vigor. Observation lines of triangulations used by him reached the length of almost 200 miles—a feat at that time "unique in the history of geodesy," as the Superintendent of the Coast and Geodetic Survey approvingly stated.

The crowning achievement of Davidson's career was the measurement of the two base lines upon which the triangulation of California rests. In 1881 he measured the Yolo Base Line twice, with the result that the probable error, as computed by his collaborator C. A. Schott, was 9.57 millimeters on a line measuring 17,486.5 meters—a minimum of error probably never equaled under similar circumstances. The story of this unusual feat may be found in the U. S. Coast and Geodetic Survey *Reports* of 1882 and 1883. In 1888–1889 Davidson repeated this performance by measuring the Los Angeles Base Line three times.

The final achievement of the Coast and Geodetic Survey during Davidson's incumbency was the definite establishment of the California-Nevada boundary. California's boundaries with Oregon and Mexico had been established without difficulty, though not without error. The Nevada line remained for several decades a problem. Captain Sitgreaves began the survey in 1852, G. H. Goddard continued it in 1855, J. F. Haughton ran the line from Lake Tahoe to a point east of Mono Lake in 1863, and James Lawson extended it to beyond White Mountain. In 1872–1873, San Francisco's pioneer engineer, A. W. von Schmidt, finally ran through the entire line. After the Coast Survey had been placed in charge of the inland triangulation, an error was discovered in checking the initial starting point at Lake Tahoe. In the final survey, begun in 1893, von Schmidt's line south of Lake Tahoe was moved west several miles.

The total solar eclipse of January 1, 1889, helped to augment the interests of Californians in astronomy. About six scientifically equipped parties and numerous amateurs observed the phenomenon. The Astronomical Society of the Pacific was organized the same year. Well supported, it soon became one of the strongest organizations devoted to science.

In 1894 the second mountain observatory was erected north of Pasadena on Echo Mountain, a shoulder of Mount Lowe, at an elevation of about 2,500 feet. The telescope was a 16-inch refractor, with which Lewis Swift, its owner, had discovered 960 nebulae and nine comets in Rochester, New York. During the next six years, as director of the Mount Lowe Observatory, Swift discovered 230 additional nebulae and five other comets.

The third observatory to be established on a California mountain is on Mount Wilson, 5,710 feet above sea level. It was upon S. P. Langley's recommendation that the Carnegie Institution of Washington provided the funds for the establishment of this observatory. Langley, the director of the Allegheny Observatory, had done extensive work in solar radiation and wished to check the influence of the vapor and dust content at low altitude as compared to conditions at very high altitude. "A southern latitude," he wrote to Davidson on May 30, 1881, "dry climate, and above all, clear deep blue sky. Another important thing is the provision of an adjacent station having great difference of altitude. All these conditions seem to meet at Whitney." From July to September, 1881, Langley's party, among them James Keeler, subsequently Director of the Lick Observatory, observed from three stations, Mount Whitney, 14,496 feet, Mountain Camp, 11,600 feet, and Lone Pine, 3,727 feet high. The success of Langley's party led to a number of other observations on Mount Whitney, especially after the Smithsonian Institution had erected a suitable building on the summit, the lack of which had been felt by the Langley party.

It was in 1902 that the Carnegie Institution of Washington was founded. In 1904 steps were taken by the Institution and by Dr. George E. Hale (who negotiated the first lease) preliminary to the actual establishment of an observatory on Mount Wilson. In 1905 the Carnegie Institution made the first grant for the building and maintenance of the Mount Wilson Solar Observatory. The usual controversy among astronomers had arisen about the desirability of altitude for astronomical observation. A committee of leading astronomers arrived apparently at a compromise, suggesting Mount Wilson, which had already been occupied by a Harvard University party from 1889 to 1891. At the same time the committee recommended a 60-inch reflector telescope as most suitable. Hale, the chief advocate of the reflector telescope, was appointed director. With that a new phase in the history of astronomy was ushered in, and California was again in the lead.

In 1898, James E. Keeler, Director of the Lick Observatory, had already shown the superiority of the reflector for discovering nebulae and star clusters by means of photography. With the comparatively small auxiliary reflector at Lick Observatory hundreds of new nebulae were discovered in a small section of the sky, which led to the conclusion that hundreds of thousands of nebulae existed and awaited discovery.

This method of observation was now employed at Mount Wilson on a larger scale and with more powerful telescopes: first a 60-inch, and then, since 1918, a 100-inch reflector. It is, of course, here impossible even to summarize the spectacular results obtained on Mount Wilson in solar research, stellar distances and velocities, spectroscopy, compositions of star clusters and nebulae, and so forth. New was Hale's idea of considering an observatory as a huge physical laboratory of which the telescope forms only one part—the most essential, to be sure.

Even before the installation of the 100-inch reflector Hale had visions of a more powerful telescope and with his energy and perseverance he went about to make his dream come true. After the usual trials and tribulations the trustees of the Rockefeller Foundation in 1928 voted the sum of $6,000,000 for the erection of a 200-inch reflector. The marvelous results on Mount Wilson had shown that the peaks of the Southern California mountain ranges offered the best atmospheric conditions for astronomical observation in the United States. Palomar Mountain, in San Diego County, 6,126 feet above sea level, was selected as the site for the new telescope, which was to penetrate more deeply into space.

Palomar, "place of the pigeons," is a remarkable orographic feature for which even the Indians had a name, "Paauw." American surveyors named it Palomar after a Mexican land grant, but generally it was known as Smith Mountain until the Board on Geographic Names restored the beautiful old Spanish name in 1901.

Hale died ten years before the completion of the great work of which he had been the chief mover. When the observatory was dedicated in 1948, the immense instrument was named Hale Telescope in his memory. The Palomar Observatory is operated jointly with the Mount Wilson Observatory by the Carnegie Institution and the California Institute of Technology. The Hale telescope together with its essential auxiliary, the 48-inch Schmidt telescope, will continue in the lead of exploring the mysteries of the universe.

Astronomy may be said to blend more with the main stream of general culture than any other science. Many of our great astronomers were not professional men but began as amateurs who took up the search into cosmic existence as a hobby, and there are innumerable other laymen who are interested in the various phases of astronomy. California has not been remiss in satisfying this interest. At Lick, Griffith, and some smaller observatories special nights are set aside when the general public may get a glimpse of the heavenly bodies and their motions. The most suitable invention to arouse the public's interest in astronomy, the planetarium, is represented in California by the Griffith Planetarium in Griffith Park, Los Angeles, and the Morrison Planetarium, a unit of the California Academy of Sciences in San Francisco. California is thus the only state in the Union which possesses two planetariums, one of which, although based on the principle developed by the famous Zeiss Works, was entirely constructed, assembled, and mounted in the shops of the California Academy of Sciences.

The great variety of California topography as well as its historic background made the State in its infancy a successful testing ground for geodetic work; climatic and atmospheric conditions, the generosity of its citizens, and the enthusiasm of its people have contributed significantly toward making California the leading commonwealth in the science of astronomy.

SOURCES

The George Davidson papers, Bancroft Library, University of California, Berkeley.

The reports and publications of the Government agencies and the institutions mentioned in the text.

W. W. Campbell, "A Brief History of Astronomy in California" in *The History of California* (1914). New York: The Century History Company.

Helen Wright, *Palomar* (1952). New York: Macmillan Co.

THE CONTRIBUTION OF NATURAL HISTORY TO HUMAN PROGRESS

By G. F. FERRIS
Stanford University

The Meanings of words quite commonly change over a period of time and a meaning that may have been current a hundred years ago may now be obsolescent or even obsolete. So with the meaning of the words "natural history." If we look back at the history of the development of biology, those words carried a meaning a little over a hundred years ago that subsumed almost everything that was then known about plants and animals, since what was then known, apart from some small amount about human anatomy as a subject entirely by itself, was mostly concerned with the questions of how many and how different were the various kinds of organisms on the earth. It considered to some small degree the manner in which those organisms were grossly put together, for a knowledge of this was involved in determining how varied they might be. Work had been done also in what we now call comparative anatomy, but this comparative anatomy, lacking the stimulating influence of the idea of evolution, really involved nothing much more, even in the work of Cuvier, than a recital that in certain kinds of animals certain structures were to be seen and in other kinds of animals other structures were to be seen, together with the idea that an animal could be identified merely by its bones or even by a single bone.

It is quite true that some other things were included merely on the fringe of natural history as thus conceived. Such was the knowledge of the cell and an appreciation of its significance, which dates only from 1839. Such was the knowledge of paleontology, which, long ago kidnaped by geology, is actually an aspect of natural history and has its beginnings in the work of this same Cuvier, who died in 1832. Such was the very slight knowledge of physiology that was all there was of this now mighty branch of biology. Some of the subjects which now occupy our attention had not yet been born. There could have been no cytology until the knowledge of the cell had been developed beyond the point of its mere recognition. There could consequently have been no such thing as histology until the aggregation of cells into tissues had been grasped. There was a bit of embryology, going as far as macroscopic examination could carry observers, but the real development of embryology had still to come. Genetics was not then even conceived. Biochemistry was undreamed of and the various inferences to be drawn from the knowledge of how many and how various are the forms of organisms were just beginning to germinate in the minds of naturalists.

So the naturalist as he existed, at least almost to the middle of the nineteenth century, was primarily, if not almost exclusively, a man who had a knowledge of as many different kinds of animals or plants as possible and who knew something of what could be learned about these organisms by observations made in the field. He was a man characterized above all by the range of his interests, which might encompass the entire field of natural history. He was the man who is referred to now, sometimes with respect, sometimes with a sort of envy, and sometimes with a slightly condescending air, as the "Old Time Naturalist." The race existed until well into the early years of the present century; some of its members have died only within the last few years. Now with the passing of the last few stragglers it is extinct or so nearly extinct that at the most it constitutes a "relict species." The intellectual climate has changed and it is perhaps as well for their own sakes that the "Old Time Naturalists" are gone. They would not be comfortable in the present climate! The environmental pressures are too great!

Here is an example of the alteration of a species brought about by changes in the environment. Natural history has changed to meet the demands of the new environment and naturalists have either disappeared or altered their outlook to meet the new conditions.

Continuing this method of nomenclature, these "Old Time Naturalists" have been replaced by what, at the best, might be called the "New Time Naturalist." He is a modification of the earlier form, a derivative of it, but modified to succeed in this new climate. He has of necessity become a specialist in some one or more of the many subdivisions into which the old field of natural history has been fragmented; but he retains something of the spirit of his predecessor and some vision of the freedom with which that predecessor roamed at will over his domain. There are a few men still who deserve the distinction of being thus listed in the line to which the "Old Time Naturalist" gave rise. But alas! Even they are now relatively few and perhaps lonely. They have, of necessity, largely themselves been superseded by the "narrow specialist," whose interest is bounded by a fence surrounding one of these fields or fragments of the fields into which natural history has been shattered and subdivided, fields that all too often are surrounded by a fence "hog tight, bull strong, and horse high"[1] through which they cannot escape, even if they would. They have been conditioned to accept their fate and seek for no other.

But there are signs that these fences may be in part crumbling and of recent years there have been indications that still another breed is rising, a second generation in which the recessive or suppressed characteristics of the F_1 generation are now reappearing in the F_2 generation. There are now an increasing number of men in biology who recognize that restriction to these narrow fields is neither comfortable nor desirable and who have begun the task of reintegrating them into fields of larger dimensions. Perhaps those reintegrated fields are not yet as large as was the old natural history, but there are indications that in time they may become even larger and more productive. Here, as is the nature of wheels, the wheel begins to come back full circle but farther along.

So it is perhaps a propitious time at which to consider what the contribution of natural history to human progress has been in the past, in part as an aid to developing an appreciation of what was done and in part as an aid to the appreciation of what may still be done by one who refuses to be confined within a narrow specialty.

1. A characterization derived from advertising contemporaneous with the last days of the Old Time Naturalists and the early days of the author as a farm boy.

The Legacy of the Old Natural History

What of the old natural history was there that may be carried over and legitimately included within the field of consideration of the new natural history? Shall we limit the applicability of the term itself to the activities of the period up to roughly 1900, when it had a certain generally accepted meaning, or shall we extend it to include at least some of the derivatives that have developed during the last part of the nineteenth century and the first half of the twentieth? On the one hand, we risk limiting it too much; on the other hand, we risk extending it beyond any acceptable limits. For one thing, the earlier natural history was certainly not co-extensive with all of what we now call biology and even many of the special fields of the present day are certainly not entirely devoid of what we might call natural history. If we search for the common element, we may at last come to the solution that what we wish to find is to be sought for not so much in content as in an attitude of mind.

This attitude of mind has been discussed by Marston Bates in his delightful book *The Nature of Natural History.* It is in brief, the attitude of mind which displays interest primarily in the organism as a functioning whole and as a part of the living world. With such a conception, the person who is interested only in the permutations and combinations of the chromosomes within cells may call himself a biologist, but he is certainly not a naturalist—a fact upon which he would probably pride himself. But as soon as he begins to think about these chromosomes and their permutations and combinations in conjunction with the influences from the world around them, his thoughts begin to impinge upon natural history, upon the fate of the organism which contains the chromosomes as it has to accommodate itself to the facts of life. He begins to think of the organism as a whole. The physiologist who is interested only in the processes which go on within the membrane that surrounds a cell is certainly not a naturalist and—if my observation of such individuals is at all correct—is not at all disturbed by that fact. But when he begins to think about these cells as organized into a complete plant or a complete animal, he must begin to think at least a little about how this plant or this animal is going to live in company with and in competition with other plants or animals. He begins to show some faint indications of the mental processes of a naturalist.

On the other hand the thoroughgoing naturalist of the old style suffered certain limitations. His interest may have been confined entirely to the organism as a whole, to the complete ignorance of the processes going on within the organism and upon which its outward functioning as a whole depends. He accepted the fact that there is such a thing as heredity but was not much concerned with just what heredity implies concerning the processes by which a character is passed on from one generation to another. Concepts of processes being involved in this functioning—processes of respiration, processes of the utilization of food, processes of excretion, processes of nervous stimuli and the transmission of those stimuli, processes by which cells arise and divide and tissues are formed, processes by which substances are transferred from one cell to another—these were entirely beyond his ken and hence beyond his interest.

So, as knowledge of these processes began to appear and to increase and the need for a detailed factual understanding of them became apparent, the naturalist commenced to lose his hold upon the body of knowledge that was developing. It began to go beyond his immediate horizon. He became more and more restricted to observation of what can be seen or inferred only from the complete organism, without any regard to what goes on within it or to the way in which what goes on within it conditions its activities. He himself began to build a fence around his own thinking as it were and finally to lose all connection with the workers in these special fields.

Conversely, the knowledge of these special fields ultimately came in many instances to be so detailed that it seemed almost beyond the range of any one person to grasp more than one of them. Not only was natural history crowded out but also the specialized fields began to elbow each other. Witness what happened to comparative anatomy, which is the term generally used if one is studying the structure of vertebrates, and comparative morphology, a term that has come to have the same meaning if one is studying certain invertebrates. The great era of comparative anatomy began with Cuvier in the early years of the nineteenth century and lasted to about 1900. During its early stages it could very well be included under natural history, but it developed into a specialty by itself and in turn came into competition with the rising studies of cytology and histology and physiology, which last was more concerned with what goes on within the tissues than in how they are put together. And at last, coincident with the rise of genetics, comparative anatomy almost faded from the scene.

During the rise of the various specialties in biology great masses of detailed information have been accumulated, making it difficult for anyone not immediately concerned with these specialties to master their content. This has been seemingly inevitable, for the first necessity in the development of any field is merely to accumulate facts. Eventually, however, these facts lead to the development of theories and principles and then to a degree of simplification. The pertinent facts are sorted out, the principles are established, and in time a stage is reached when it is no longer necessary to have all the details at one's fingertips in order to appreciate the bearing of a particular discipline upon other disciplines. When that stage has been reached, the general student does not need to know all the details that have been worked out about the physiology of the cell, but he does need to know the principles involved. And we are coming to the point where those principles are being formulated in such a way that it is possible to grasp them and their implications for workers in other fields. In other words, we are coming to the point where the general student can begin to get an understanding of the principles that are involved in many fields and which have a bearing upon the special field in which he is engaged.

Thus the principles of genetics have a very profound bearing upon the work of the systematist especially as it concerns species. They even have a bearing upon the work of the student of comparative morphology. Conversely, the work of the systematist has a profound bearing upon the broader problems of genetics and I feel sure that the comparative morphology of the arthropods, for example, will, when well enough developed, have a profound bearing upon conclusions derived from genetics.

So we are coming once more to a situation in which the person of broad interest need not necessarily have to be a master of all the details of all these specialties. He need concern himself only with the principles—with perhaps enough knowledge of details to understand those principles. He is to a degree freed from slavery to detail. And if that be true, the naturalist can arise again and contribute as a naturalist to the progress of biology and through the progress of biological understanding to the progress of man.

There is here, however, one disturbing thought. The progress of biology has been coincident with the rise and recognition of the professional biologist. The Old Time Naturalist was in many instances a man who did not earn his living through his knowledge of natural history. The present-day biologist is generally employed in a professional capacity. Now a professional position demands professional competence and professional competence demands something more than acquaintance merely with principles. So the professional biologist who wishes to compete within his profession is forced to consider and become proficient in details as well as principles. And there is many a professional position which demands nothing more—and frequently does not encourage anything more—than competence in details. How that difficulty is to be resolved is not immediately apparent. But we may hope that the genuinely competent man who has it in him to extend the bounds of knowledge will also have it within him to triumph over difficulties and eventually to emerge from the forest of details into the high places where his view is unobstructed and far-ranging.

So as one approaches the story of the contributions of natural history to human progress it is desirable to remember something of the history which we have been discussing. Natural history has given us some great things; in the hands of real naturalists it can still give us great things. Let us consider how natural history has expanded our range of thought and how it has contributed to human progress, by this and by other means.

There are two aspects of these contributions which need to be considered. One has to do with philosophical matters, the other has to do with material or practical considerations.

Theoretical Aspects

First as to philosophical matters. Out of the work of the Old Time Naturalists came the beginnings of most of the great ideas that not only dominate biology today but reach far beyond.

Consider the concept of evolution, the men from whom it came and the men who first of all rose to its support and establishment. This was purely a contribution from natural history; physiology had nothing at all to do with it. Experimental biology had only an infinitesimal connection. Biochemistry had nothing to do with it. Cytology had nothing to do with it. Comparative anatomy had only a small part. Genetics had nothing to do with it, for genetics was not yet conceived, even less born. Natural history, in its purest form, was almost all that existed of what we call biology at the time when the idea of evolution was accumulated in the minds of Darwin and Wallace and their predecessors. The idea of evolution arose in the minds of men whose knowledge of any aspect of what we now call biology except what was included in natural history was almost nil. Their predecessors, Buffon, Lamarck, and Erasmus Darwin, were purely naturalists. Wallace, who shares with Charles Darwin the honor of first formulating a definite and intelligible concept of how evolution could have been brought about, was a field collector of insects. Charles Darwin himself was the purest of pure naturalists, whose ideas concerning evolution were first developed in the course of his voyage about the world collecting and observing objects and phenomena with the eye and the interests of a naturalist. He was indeed a naturalist in the oldest and most uncontaminated meaning of the word. His interest was in animals and plants as complete and functioning wholes, living with other animals and plants, themselves complete and functioning wholes. The impact of this idea of evolution has been felt not only in biology, of which it is the great and unifying idea—indeed the greatest idea that has been contributed to human thought—but it extends into every field—philosophy, theology, sociology, even politics. Its influence extends indirectly even into the newest of all fields, nuclear physics; indirectly into this last field, since the idea of organic evolution has broadened into a concept of inorganic evolution as well, and nuclear physics has contributed to the idea of the transformation of one element into another as an accepted and established process. The idea of a physical world which is not static but is forever changing and evolving is made possible by the prior establishment and acceptance of an organic world that is changing and evolving.

The evolution of life and the evolution of nonliving matter are no longer separate and distinct things but are merely parts of a continuum. The idea of organic evolution gave cogency to the thought that for this evolution time was needed and the realization of the need for this time undoubtedly influenced the thought that time must be found. From a world that was perhaps a little more than five thousand years old to a world that is probably two billion years old and on which life has existed for probably five hundred million years—that is the measure of the influence of an idea which sprang from the activities of a naturalist! That is the measure of the foundations which natural history of the nineteenth century laid down for us.

What difference does it make that Darwin knew no physiology, no cytology, no histology, no chemistry, no experimental biology, no biochemistry, no genetics, no nuclear physics? All that counted for the development of his great idea was the fact that he had some appreciation of the richness of life upon the earth and some appreciation of the fact that all these organisms live in a world of other organisms with which they must compete. The remainder is the development of inferences to be drawn from this recognition and the development of the techniques necessary to investigate the facts. Most of this work would probably have been done even if the idea of evolution had never been brought forth, but the idea of evolution gave a guidance and a direction to the whole process that would otherwise have been lacking. Without this central theme one can conceive only of confusion resulting from all this uncoördinated activity.

In the ancient religions of the Mediterranean world and the Near East there recurs time after time the concept of the "Great Mother" and we see this concept continued today in what some students regard as a lineal succession in one of the predominant religions of the western world. Cybele, she was once called, this "Great Mother." If a biologist were to accept this idea as having had an influence on the development of biological thought and were to seek her name it might justifiably be accepted as natural history, which was the great mother of all the branches of investigation and thought which we now place under biology. These branches are her children and her grandchildren, and we can even see something of the gestation, at least, of her great-grandchildren.

It is perhaps here that natural history has its chief claim to our respect. As the great mother she was the founder of a dynasty. With all her weaknesses, with all her deficiencies, with all her naïveté, with all her actual ignorance of many things, she was still great. She is now old and feeble and condemned to withdraw from the main stream of activity, but the memory of her former greatness still remains. It is in her children and grandchildren—by direct descent and as they have been hybridized with other lines—that we must seek to continue this résumé of her influence upon human progress. That lineage is beginning to become involved, somewhat like the lines of descent of ancient royal families.

Practical Aspects

Of her children the one which most closely resembles its parent is ecology. In fact, there are those who would say that ecology is merely natural history under another name. Were that entirely true, we would have something analogous to the history of the gods and goddesses of mythology, many of whom changed their names but not their attributes. But natural history lived and flourished before the days of fingerprints and so a positive identification of ecology with natural history cannot very well be established. We may make a concession to the desires of ecologists who wish their subject to have the dignity of an identity all its own. Let it rest. Let them have that dignity, but let them not forget who was their maternal parent.

Here, if anywhere, the need for considering the organism as a whole, living in a world of other organisms functioning as whole, still remains. In fact that is what ecology is by definition, "the relation of an organism to its environment" both living and physical. True, there is a branch of experimental ecology which follows the experimental technique of bringing the subject of study into the laboratory, dissociating it into its component parts and studying each of these parts—temperature, moisture, pressure, light—as a thing by itself with the hope eventually of combining these things in various degrees and then submitting the combinations to similar study. This branch of experimental ecology is almost a grandchild of natural history, for it is a hybrid involving elements from physics, chemistry, and statistics. It displays something of that "hybrid vigor" that is often talked about, but as yet it is merely a strong and active child. Ecology in general is still based upon the necessity for actually going out into the fields and the woods and the waters and observing what is going on. The ecologist may at times don his white jacket, retire to his laboratory and listen to the music of a computing machine, but by and large, withal, he will be working up the data that were initially obtained while he wore a pair of field boots and was engaged with the activities of plants and animals as they live in company with each other, subjected to the wind and the rain, to heat and frost, and to the rolling seasons. The ecologist of today may use registering thermometers and improved rain gauges and barographs, improved methods of obtaining population counts—and above all, improved means of transportation that prevent blisters on the feet—but the objective and the outcome are in spirit very much the same as they were years ago in the days of natural history. I go along with Marston Bates who remarks that "both labels apply to just about the same package of goods."

Even if an ecologist might object to being called a naturalist, he would surely not object to being included in a survey of what natural history has done for human progress. There is here, however, actually a defining line to be drawn.

Natural history, as has been pointed out, made some great contributions to philosophy. Ecology has made, and above all has the potentiality for making, some great practical contributions. There are two aspects in which this last is clearly apparent. One of these is connected with the conservation of renewable resources. The other aspect concerns the application of ecology to medicine.

We are confronted at the present time with a growing realization that our renewable resources need to be studied. Our forests are beginning to show signs of wear from use. Our wild food animals from sardines to ducks and trout—if we may by courtesy include the last two as "food animals"—are showing signs of depletion. Our soil is suffering from improper handling, which, at least at times, implies improper treatment of the natural covering of grass and woodland. Any solution of these problems depends in the first instance upon a basic knowledge of the plants and animals involved, how they maintain themselves, how they reproduce, their requirements, how they fit into an environment that can maintain a balance between their numbers, the food supply that they themselves must have and the food supply that they may yield.

It is only within recent years that any appreciation of the idea that these problems are fundamentally problems in ecology has begun to develop even among biologists. This is because they have very commonly been approached from some other point of view, such as that of the commercial fisherman, the lumberman or the farmer desirous only of obtaining an immediate return from his activities. But the idea that any proper approach to such problems must rest upon a knowledge of the organisms involved is beginning to grow and eventually must become dominant if these problems are to be solved in any satisfactory way. In this lies one of the greatest contributions to human welfare that are still to be made by any subdivision of biology.

In the relation of ecology to medicine we have a very special situation. A physician is of course primarily concerned with what goes on in the human body and the relation of the doctor's activities to ecology is in many instances more or less remote. It is in connection with diseases of parasitic origin or diseases for which transmission is dependent upon other organisms that his activities come into contact with ecology. Now it so happens that the physician was at one time solely responsible for the development of our knowledge concerning these diseases. He was concerned with the effects of such diseases as malaria upon the human body, and it was entirely natural, in fact, inescapable, that he should search for the pathogen and explore the problem of how that pathogen gets into the human body. But, since he was the first to inquire into these questions, he quite naturally took over first of all a consideration also of the organisms which act as vectors for these diseases. Since it is hardly compatible with human nature to let go a hold that has once been established, the physician continued for some time to include these vectors within the range of his special domain, although he was scarcely qualified by his training to maintain this hold. In fact, the problem of the relation of these vectors to the pathogen and to man is not a medical problem at all except as medical men may be interested in preventive medicine. If I may employ an analogy, consider the instance of injuries from automobile wrecks. The doctor has to treat these injuries and he may become impressed, in the course of his duties, by the need for some procedure which will reduce the incidence of wrecks. But the problems involved in handling traffic, designing highways to minimize accidents, formulating and administering laws which will aid in doing so—these are not problems for the doctor at all.

So with these diseases of parasitic origin or parasitic transmission. Until the parasite is present in the body of man, it is beyond the range of the physician's activities and even beyond the range of his proper interest except in so far as a knowledge of this sort broadens the scope of his understanding. How to control these parasites is properly no part of his concern, for it embodies problems that are not within the range of a hospital-trained medical man. These problems are actually those of ecology, of an understanding of the insect vectors and parasites themselves, their ways of life and their relations to other organisms.

This idea has finally begun to penetrate even into the minds of doctors, and there is a growing body of men whose training fits them especially to deal with these organisms. They have no collective or corporate name at the present time, but one may safely predict that such a name will finally appear. They are scarcely to be called sanitarians. They are not strictly parasitologists. They are not necessarily medical entomologists. Just what are they? That remains to be determined, but in time some term will inevitably appear that properly indicates the range of their activity. They are actually naturalists. Personally, I am inclined to the opinion that the term "environmental medicine" could in some way be employed for their field.

But, regardless of what they may eventually be called, it is clear enough that their activities have a large part to play in the future story of human progress. The activities in which they engage have already almost eliminated from some parts of the world diseases which once made those areas relatively unhabitable by man—witness especially yellow fever—and they promise to do the same for even greater areas. In fact, it seems reasonable to predict that the control of parasites and their vectors will eventually lead to making habitable and useful to mankind those great areas of the tropics which now maintain but a scanty population and contribute but little to the commerce of the world. Whether or not this is actually a consummation devoutly to be hoped for is another matter.

Systematics

Another child of the first generation derived from the Great Mother, natural history, is biological systematics, which, as I have pointed out, at one time constituted a very large part of natural history. It was the question "How many and how varied are the kinds of organisms?" with which the naturalist was concerned. Now, however, it has become merely a section—sometimes a strongly fenced-off section—of the activities which we have inherited. It has a rather peculiar history. Originally, in a rapidly expanding world, it amounted to but little more than an expression of curiosity aroused in large part by the great numbers of previously unheard-of kinds of plants and animals that were discovered and it became to a large extent merely an attempt to give these plants and animals names and to arrange them into some sort of system by which knowledge concerning them could be handled. From this there grew what became at times almost a cult, embodying the idea that it was the sole purpose of the systematist or taxonomist to find and name as many as possible of these animals and plants and to fit them into the system. In fact, it became somewhat the idea—although perhaps never clearly expressed—that this goal extended to naming *all* the animals and plants of the world. This was contributed to by the circumstances that systematics lends itself nicely to the gratification of that instinct for collecting which is so deeply embedded in our minds. What collector of postage stamps has never dreamed of possessing a *complete* collection of all the postage stamps that have ever been issued? Or, if the impossibility of achieving this goal is too evident, has not relished at least the possibility of obtaining a *complete* collection of those stamps within the specialized field to which he restricts himself?

So this cult of finding and naming all the kinds of plants and animals of the world and of squirreling them away in collections drifted away from any special thought about the bearing of these activities upon biology. It drifted away from the desire to know anything much about these subjects of its interests. In the desire to possess collections it became concerned primarily with the collections themselves and their possession and in so doing it became at least as detached from biology as the collecting of postage stamps is detached from the primary functions of the Post Office Department. It became a subject that could be engaged in without previous training by children, retired army officers, policemen, janitors, street-sweepers, preachers, medical men, and perhaps even politicians. Some of the objects of its interest became objects of commercial enterprise. One could purchase a collection of butterflies or beetles or shells as one can purchase a collection of stamps and there are instances on record of insects having been described merely in order to increase the list of collectors' desiderata.

And yet even this expression of the collector's passion was not without its influence upon the development of natural history for, through it, men came to know something of and to appreciate the richness and the variety of life. Incidental this may in part have been, yet the indirectly beneficial result is clear. Linnaeus, the patron saint of biological systematists, knew less than ten thousand kinds of animals for the whole world. Today we know—or it may be more truthful to say know of—something up toward one million and we have reason to suspect the existence of as many as perhaps ten million kinds of animals alone, not to mention the kinds of plants.

Reflect for a moment! A biology based upon the existence of but ten thousand kinds of animals in the world would be on a very different philosophical basis from a biology based upon a concept that allows for the existence of ten million kinds. With only ten thousand kinds in the world one could almost accept the literal truth of the story of the Ark! With only ten thousand species of animals in the world one would not be confronted with the necessity of examining the multiplicity of physiological processes and phenomena that we know to exist. With only ten thousand species of animals in the world the concept of a special creation for each might well be acceptable. In other words, the idea of evolution is necessary because this multiplicity of forms demands it and makes it the only idea that the reason of a scientist can accept as offering any basis for some final understanding of the facts.

But after all, not all systematic biology has been entirely motivated or limited strictly by the mere gratification of the collector's instinct. After all, men had to go out into the world to collect these animals and in doing so they became at least to some degree acquainted with their ways of life. And so a knowledge of the occurrence and the habits of animals and plants grew up along with—possibly to some degree merely as a by-product of—this search for new species.

Above all was this true of the earlier explorer naturalists. So a very large body of information that went into the development of early natural history grew up in this way. In fact, all of these things really went together, for a person finding a strange plant or animal naturally wished to talk about it and he could not very well do so with any definiteness unless he had some sort of name for it. It was only later that a knowledge of the kinds of plants and animals moved to the laboratory and became at times completely detached from the natural world.

It was out of this combination of the knowledge of plants and animals as things living in the natural world and the describing and naming of them by what came to be called the "closet naturalist" that there came the ideas which led to that great philosophical concept, evolution. Darwin himself was a great field naturalist, but he did not disdain the work that had to be performed, for example, on barnacles in his study. He was that very desirable combination, a field naturalist and a closet naturalist.

So the mere describing and naming of the different kinds of animals had its place in the development of those concepts which, broadened and deepened, led to biology as we know it.

But apart from these philosophical concepts biological systematics has had a profound effect in the development of other aspects of biology. After all, it is at least intellectually satisfying to know what the world was like in past ages and our knowledge of what the world was like depends upon historical geology. Historical geology in turn rests upon paleontology and paleontology rests upon a study of the kinds of animals and plants that existed in the past and have come down to us as fossils. Here the recognition of the various kinds is nothing more than an extension of the knowledge of present-day species embodied in systematic biology. Any conclusions as to what the world was like when these fossils lived must be based upon observations of how similar kinds now live. If fossil plants are found which are known only from tropical regions, it is a fair assumption that these fossils must have been laid down under tropical conditions. So, reasoning from the conclusions concerning the kinds of organisms involved and field natural history concerned with the habits of similar organisms, we come finally to some understanding of the climates of the past. Thus another step is taken in broadening our outlook on the world.

Biogeography: Another matter that has at least an intellectual interest as well as some practical concern is the problem of how animals and plants are arranged naturally about the world. This is what is known as biogeography. It depends entirely upon the results of systematics. The data utilized are merely those of systematics, further systematized by embodying them in maps of the world or portions of the world. The validity of its conclusions depends, then, upon how well the world has been explored and how well the systematic work has been done.

The practical aspect of this may be indicated by examples from economic entomology. Let us say that a hitherto unknown pest is found in the United States—as has happened many times. For various reasons we wish to know where that pest came from. Some of these reasons are merely concerned with satisfying curiosity, others with practical considerations. In entomology that practical consideration has to do with the question of what we call "biological control," which is an aspect of applied ecology. We know that in its natural habitat an insect has certain enemies which control its numbers and that, if we could introduce those natural enemies into the area now infested by the insect, we might be able to restore the balance that existed in the land of their origin. But to search blindly for these natural enemies with no idea of where they are to be found is a wasteful business. Sometimes that has been done, and on a few occasions the search has, by great good fortune, been successful. On some other occasions it has failed. Thus expeditions searching for natural enemies of the "red scale"—an insect of much economic importance to the citrus growers of California—were sent to South America, to Australia, to Africa. They secured no parasites that were effective against the red scale. Why? The red scale, we now are quite sure, is a native of southeastern Asia.

How do we determine purely from sytematics where an animal came from? First of all, there should be a study of the great group to which the animal belongs—let us say, in this case, scale insects. By this study we arrive at an idea of the minor groupings that exist. Next by a study and a mapping of the distribution of the species of a minor group we determine what part of the world it belongs to. Then, by a more detailed study of all the species contained in this minor group, we arrive at an idea of where a particular species naturally belongs. Finally we can put our finger on the map of the world and say, "This is the most probable place in which a search for parasites would be profitable." A study of this sort indicated that parasites of the "olive scale," an insect of importance in California, would most probably be found in northwestern India or Persia. A search guided by this information found parasites in India, which have been introduced into California and promise to be of value.

In the field of that "environmental medicine" already discussed the systematics of mosquitoes has demonstrated its value. Only certain species of mosquitoes carry malaria, while different species carry yellow fever and other diseases. It is useless to spend money for the control of these diseases by attempting to control "the mosquito." There are hundreds of kinds of mosquitoes, and the recognition of the particular mosquito concerned is essential if our efforts to control the disease by controlling mosquitoes are to be properly directed.

Paleontology: There is one other field worthy of some special consideration in which biological systematics has a very practical contribution to make. That is the field of paleontology, which is fundamentally the recognition of the different kinds of animals and plants that have lived in past times and that have left fossil remains in the rocks. Paleontology could possibly be regarded as purely a consideration of these fossils, but that would be relatively unprofitable and it is well that it merges with, and is united with, information from other fields to become historical geology. Historical geology has had not only a profound influence upon the development of the idea of evolution but also upon many practical matters. Time was when this was about all the explorer searching for oil had to depend upon, although it is now aided and abetted by other methods, but the practical aspects of historical geology still exist.

These are merely pertinent examples, which could be multiplied many times, to show that biological systematics has a proper place and at times is essential to the development of a proper understanding of the world in which we live.

In the end the systematist, if he is to fulfill his possibilities of being helpful to mankind, must think of his specimens as being merely samples of great populations living out of doors under natural conditions. This systematist may sit at his microscope or his desk working only with the variously preserved remains of his specimens, but if he has any vision of his place in the great endeavor to improve the world, that vision must reach far outside the walls of his study or laboratory—and does.

So biological systematics still has a place as a part of the great endeavor that has as its goal human progress—progress intellectually and progress in more immediately applicable things. It still maintains its former place of importance in natural history, for it furnishes the material with which a naturalist must work. The ecologist, the student of geographical distribution, the student of biological control, and even the student of genetics—especially with reference to the origin of species—must make use of its findings. Systematics may change—and it is to be hoped that it does change—from concentrating its attention so much upon "new species" to concentrating primarily upon the problems of classification and upon its liaison with other branches of biology and the contributions that it may make to such general problems as those having to do with the mechanism of evolution, but its continuing place is secure.

Genetics: One of the most interesting developments of systematic biology is its liaison with genetics. During the years in which Mendelian genetics was struggling to establish its body of ascertained fact there was but little opportunity and little time to consider the relation of the implications of genetics to other fields of biology. But, with this basic body of fact quite well determined and with the underlying principles established, the opportunity has finally come and to some extent has been grasped to explore connections with other fields. One of the most fruitful of those fields is biological systematics. In the problem of how the members of a single interbreeding population become differentiated into two or more distinct and finally non-interbreeding populations genetics and systematics reach a common ground, for both have here their common interest in the matter of evolution. Thus at last there has arisen by hybridization between the offspring of natural history and that relatively recent, apparently quite unrelated discipline, genetics, a new way of approach to these common problems. This too is at present a field without an accepted name, although there is some reason to think that the name now used by some of those who are interested in such matters—biosystematics—may eventually receive a wide acceptance.

We could explore these matters further and call attention to other ways in which natural history and her lineal descendants, "bone of her bone and flesh of her flesh"—if we may revert to an ancient phrase—have contributed their share to human knowledge, to the advance of biology, and to the practical affairs of life. We have, for example, not mentioned the bearing of a knowledge of the fungi which is involved in the development of what the medical man calls the "antibiotics." We have not mentioned agriculture, which involves certain aspects of ecology and which will do so more and more as the needs of the world for an increased food supply becomes more manifest. We have not mentioned—but let it rest!

In the words attributed to the mother of the Gracchi in referring to her distinguished sons, "these are my jewels," natural history has been the Great Mother of them all.

CLASSIFICATION AND TAXONOMY OF THE BACTERIA AND BLUEGREEN ALGAE

By C. B. VAN NIEL
Hopkins Marine Station of Stanford University
Pacific Grove, California

Introduction

The early 1850's as a starting point for the examination of the development of taxonomic theory are appropriate not only because of the centenary aspect of the Edinburgh meeting of the British Association but also because they have an intrinsic importance as the culminating point of pre-Darwinian taxonomy, when the natural system had triumphed completely over the Linnean.—Gilmour, 1951, p. 400.

It might be suggested that a few simple changes in the quotation above, such as the substitution of "California Academy of Sciences" for "Edinburgh meeting," would render it applicable to the present chapter. This, however, is far from true. The fact is that a century ago there did not exist even a rudimentary taxonomic theory for the bacteria. And it is highly questionable whether at present we have advanced much beyond the equivalent of a Linnean system. Nevertheless, advances there have been, though hardly in the sense meant by Professor Gilmour. Rather have they been concerned with a clearer appreciation of the problems inherent in the classification and taxonomy of the bacteria and bluegreen algae.

The following essay is intended as a sketch of the main trends of these developments. It does not contain a detailed description and discussion of the various systems of classification of these organisms that have been proposed in the course of the past century. Information of this sort can be found in various text- and handbooks; Migula's *System der Bakterien* (1897–1900) and his contribution to Lafar's *Handbuch* (1904–1907), Buchanan's *General Systematic Bacteriology* (1925), and Bergey's *Manual of Determinative Bacteriology* (6th ed., 1948) trace them satisfactorily for the bacteria, and Geitler's extensive treatise on the bluegreen algae (1932) comes close to performing this task for the latter group.

The Natural Affinities of Bacteria and Bluegreen Algae

Quoi qu'il en soit, les Schizomycètes ne sont point une classe. Une classe de quoi? ai-je demandé au Comité International de Nomenclature à New York en 1939; et aucun des nombreux délégués représentant le monde bactériologiste n'a pu répondre. C'est au moins un embranchement, mais un embranchement autonome, intermédiaire entre les règnes animal et végétal et nettement séparé d'eux. Pourquoi ne pas avoir le courage de dire: le Règne Bactérien?—Prévot, 1940, p. 10.

Although first seen and described nearly three hundred years ago by Antonie van Leeuwenhoek, bacteria could not be adequately studied, for lack of an appropriate methodology, until the second half of the nineteenth century. Nevertheless, some of the general features of the organisms, such as the occurrence of motile forms, and multiplication by transverse fission, had been established, and the discovery of the bacteria had raised the question whether they ought to be regarded as plants or animals.

Prior to 1854 their animal nature had been taken for granted, locomotion probably being the chief criterion on which this belief was based. But in that year Cohn (1854) argued in favor of a close relationship with plants, especially with the bluegreen algae. Following Nägeli's introduction (1857) of the name "Schizomycetes" ("fission fungi") it became customary to use this term, with the ending appropriately modified to indicate the status as a family, order, or class, for the collective designation of the bacteria. Along with this practice the notion of the plantlike nature of the organisms gradually won ground.

It cannot be denied that there are good reasons for subscribing to this view. Especially the existence of an autotrophic mode of life among the bacteria may be considered a strong point in its favor. The chemo-autotrophic sulfur bacteria of the *Beggiatoa–Thiothrix–Thioploca* group in particular form a striking example because also from a morphological-anatomical point of view they show their plantlike nature; the structural similarity with the bluegreen algae of the family Oscillatoriaceae is great indeed (Pringsheim, 1949). The green and purple sulfur bacteria, and the brown and red nonsulfur bacteria resemble the plants even more closely in physiological respect by virtue of their photosynthetic ability. Recently it has been proposed that the chemo-autotrophic mode of life can be envisaged as a precursor of the photosynthetic one, and that such processes as characterize the photosynthetic bacteria would represent a logical link between chemo-autotrophy and green plant photosynthesis (van Niel, 1949a).

In spite of these rather compelling considerations, doubts as to the exclusively plantlike nature of the bacteria have also been expressed, and this with increasing frequency. It should be emphasized that Nägeli had not in the least committed himself concerning the general relationships of his Schizomycetes; this is evident from the statement (Nägeli, 1857, p. 760):

> Ueber die Bedeutung der Gruppe Schizomycetes, ob es Pflanzen, Thiere, oder krankhafte thierische oder vegetabilische Elementartheile seien, darüber giebt die anatomische Struktur keinen Aufschluss, dass es Pflanzen und keine Thiere sind, dafür liegen wenig Gründe vor.

The vast increase in our knowledge of "the bacteria" gained during the past century has not made Nägeli's statement obsolete. This must in part be ascribed to the difficulty of finding close affinities of certain bacteria with specific taxonomic groups among the plants. While F. W. Andrewes, for example, states (1930, p. 298):

> . . . It was not till the middle of the nineteenth century that first Naegeli and then Cohn proclaimed the vegetable nature of the bacteria. So gradual is the transition from the mould-fungi, through the streptothrix group and the acid-fast bacteria, to ordinary bacteria, that there are few who do not agree with Naegeli.

it is equally true that relationships with bluegreen algae and with other groups of organisms can also be defended on reasonable grounds. The quotation from Prévot at the beginning of this section clearly reveals this difficulty. And from a phylogenetic standpoint it is hardly surprising that a major problem would exist; it is, in fact, inherent in the concept of evolution itself.

Acceptance of the doctrine of organic evolution implies that the clearly recognizable forms of plant and animal life must have had a beginning in some far more primitive ancestry. It does not appear unreasonable to envisage the evolution of an elementary "molecrobe" to typical plants and animals, respectively, as having passed through intermediate stages of increased complexity which, in a number of respects, would have the characteristics of "bacteria." Such intermediate stages are themselves neither plants nor animals; they occupy a position in the realm of living organisms that is antecedent to the emergence of the later developmental stages, and display characteristics of both major kingdoms. It is not the contention of this argument that the present-day bacteria are, in effect, such intermediate stages; it is easily conceivable that they might represent organisms that have evolved from the same precursors from which also the typical plants and animals, by different routes, originated.

As early as 1866 this situation was clearly recognized by Haeckel, who wrote (1:202–203):

Wir finden in den bekannten Thatsachen durchaus keine Nöthigung für die Annahme, dass alle Organismen-Stämme entweder Thiere oder Pflanzen sein müssen. Vielmehr müssen wir die bisher gültige exclusive Zweitheilung in Thier- und Pflanzenreich in dieser Beziehung für nicht begründet erachten. Es ist schon von verschiedenen Seiten darauf aufmerksam gemacht worden, dass es sowohl für die Zoologie als für die Botanik ein grosser Gewinn sein würde, wenn man die vielen zweifelhaften Lebewesen, die weder echte Thiere noch echte Pflanzen sind, in einem besonderen Mittelreiche oder Urwesenreiche vereinigen würde; doch hat unseres Wissens noch Niemand den Versuch gemacht, ein solches neues Reich der Urwesen nach Inhalt und Umfang fest zu bestimmen, und seine Begrenzung wissenschaftlich zu begründen und zu rechtfertigen. Wir wagen hier diesen Versuch auf Grund der obigen Deductionen und schlagen vor, alle diejenigen selbstständigen Organismen-Stämme, welche weder dem Thier- noch dem Pflanzenreiche mit voller Sicherheit und ohne Widerspruch zugeeignet werden können, unter dem Collectivnamen der Protisten, Erstlinge oder Urwesen, zusammenzufassen.

In this new kingdom the bacteria, along with such dubious organisms as *Protogenes* and *Protamoeba,* were allocated to the first phylum, Moneres, comprising, in Haeckel's words, "the completely structureless and homogeneous organisms which consist solely of a bit of plasma (a mucoid protein compound), obtain their nutrients simply by endosmosis, and reproduce by schizogony or sporogony" (1866, 2:20).

Unquestionably there is much that can be said in favor of Haeckel's third kingdom. Nevertheless, its acceptance raises a new problem to which F. W. Andrewes (1930), following Kent (1880–1882) and Bütschli (1880–1889), has called attention in the statement (p. 298):

To revive Haeckel's third kingdom of "Protista" for organisms so low down in the scale that they cannot definitely be assigned to either of the other kingdoms, may be a useful expedient, but it is a doubtful gain, for it necessitates two arbitrary lines of demarcation in place of one.

The seriousness of this problem becomes at once apparent when one considers the extreme paucity of characteristics which one is compelled to associate with the early forms of life, the pre-plant and pre-animal organisms for which the kingdom Protista was proposed. Morphological and developmental features must here be so primitive that they can hardly be expected to serve as a useful guide in determining phylogenetic trends and relationships. Haeckel, realizing this, had had recourse to physiological properties as well, a practice which led him to incorporate the bluegreen algae, as photosynthetic organisms, in the plant kingdom. As a result, the views of Cohn in respect to the close affinity between the bacteria and the bluegreen algae did not come to a clear expression in Haeckel's system.

Since it was Cohn who, in 1872, took the most significant steps toward the development of a more detailed classification of the bacteria, it is understandable that in these attempts he adhered to his notion that the bacteria are *bona fide* members of the plant kingdom. And Cohn's influence has been so great that for a long time Haeckel's proposal was not seriously considered, at least by the bacteriologists.

But Copeland, in an important contribution, reexamined the arguments in favor of Haeckel's ideas and conceded their soundness (1938, p. 384):

> It is an ancient and familiar hypothesis, too widely accepted as a law of nature, that every living creature is and must be either a plant or an animal. Judged by knowledge and theory which were available to Linnaeus, this hypothesis is sound; judged by modern knowledge and theory, it seems untenable.

As he further pointed out (*ibid.*):

> Various authors more recent than Haeckel have shown a disposition to recognize more kingdoms than two, but none of them, apparently, has formulated a system including all organisms. Pending such an accomplishment, the old system of two kingdoms has persisted for want of a workable substitute.

With a view to improving this situation Copeland developed a substitute in which four kingdoms were recognized: Monera, Protista, Plantae, and Animalia. The first phylum of Haeckel's Protista was here raised to the rank of an independent kingdom, the criterion for inclusion in this taxon being "organisms without nuclei, the cells solitary or physiological(ly) independent. Groups included, bacteria and bluegreen algae" (p. 416). In this manner a seemingly unambiguous separation of the bacteria and bluegreen algae from all other organisms was achieved, while at the same time justice was done to Cohn's concept regarding the close relationship between the two major groups of the Monera.

Several years later Copeland returned to the problem of basic classification. At this time he stated the phylogenetic significance of the first kingdom more clearly, as follows (1947, p. 342):

> The most profound of all distinctions among organisms is that which separates those without nuclei from those which possess them. The former are the bacteria and bluegreen algae. . . . Whether or not life originated more than once, it is certain that life possessing nuclei came into existence once only, by evolution from nonnucleate life. This conclusion is as certain as any which can be based on induction: it is established by the uniformity of the nucleus, in its structure and in its behavior, in mitosis, in sexual reproduction, and as the vehicle of Mendelian heredity, wherever it occurs.

He also recognized that his designation of the kingdom as Monera was invalid because Enderlein (1925) had earlier used the name Mychota for just such a taxon. Meanwhile, the proposition of uniting the bacteria and bluegreen algae in a separate kingdom had found favor with Stanier and van Niel (1941), who had, furthermore, seen fit to expand the characterization of this unit by the incorporation of two additional, and equally negative, criteria, viz., the absence of plastids in the cells, and the absence of sexual reproduction.

However attractive Copeland's system may have appeared a decade ago, recent developments have raised difficulties great enough to threaten the very basis of the characterization of the kingdom. The most important of these deal with the problem of the "bacterial nucleus."

Even in 1938 there were some indications that bacteria contain discrete structures that might be considered, on the basis of their behavior and chemical nature, as nuclei (Badian, 1933; Stille, 1937; Piekarski, 1937). Studies of this sort have been continued, with improved methods and instruments, especially by Delaporte (1939), Robinow (1944, 1945), Knaysi (1947, 1951), Boivin (1948), Welsch and Nihoul (1948), Tulasne and collaborators (1947, 1949), and DeLamater (1952); the results support the previous allegations. Even though a convincing demonstration of nuclei has not yet been accomplished for more than a few bacterial and myxophycean types, it may be confidently expected that future work will fill the existing gap. It is thus becoming increasingly clear that these organisms cannot be incorporated into Copeland's kingdom of "microorganisms without nuclei."

Similar remarks, while not yet as definitive, may well apply to the two additional criteria mentioned above. The finding in cells of the photosynthetic bacterium, *Rhodospirillum rubrum,* of uniform spherical particles in which all the pigment is contained (Schachman, Pardee, and Stanier, 1952) indicates that plastidlike elements are not lacking in the bacteria; according to Calvin and Lynch (1952) a very similar situation is apparently encountered in the bluegreen alga, *Synechococcus.*

Last, there is the matter of sexual reproduction in these organisms. While there are some published reports alleging the occurrence of fusion of individual cells in bacterial cultures (Potthoff, 1922, 1924), these had not been taken too seriously, and it is fair to state that the actual conjugation of two cells with the formation of a zygote has yet to be observed by continuous microscopic examination. But the startlingly novel report by Lederberg and Tatum (1946; see also Tatum and Lederberg, 1947, Lederberg, 1947) of the occurrence of "recombination effects" in mixed cultures of bacterial mutants has changed the picture. The observed phenomena cannot be ascribed to "back mutations"; they are, however, readily interpretable on the basis of a postulated conjugation, followed by recombination of genetic factors during the mitotic division of the nucleus of the conjugant. It is true that the recent studies of Hayes (1952) have shown that similar recombinations occur in mixed cultures of mutants in which one of the partners has been rendered nonviable. This suggests that an unequivocal interpretation of the recombination effect as the result of a primary conjugation is not possible. On the other hand, there exists at present a healthy skepticism with regard to the earlier belief that sexual phenomena do not occur among the bacteria.

Thus it is clear that the criteria for a kingdom of organisms without nuclei do not apply to the bacteria and bluegreen algae. This does not mean, however, that the notion of establishing a separate kingdom for these organisms should be abandoned. As mentioned before, there are good reasons for subscribing to the idea that we must reckon with the existence of organisms that are neither plants nor animals and represent the descendants of precursors of both these groups.

The difficulty will be to devise adequate criteria for such a taxon; this remains a task for the future.

The Species Concept in Bacteriology

These two criteria—practical expedience in the interpretation of biological phenomena, and the application of an effective system of nomenclature—are the elements from which the systematist must fashion his concept of species.—Camp and Gilly, 1943, p. 381.

The peculiar difficulties encountered in attempts to give formal expression to the general relationships of the bacteria and bluegreen algae to other living organisms can evidently be referred to the paucity of salient characteristics among the former. This same feature is responsible for the fact that also at the other extreme end of the classification problem, concerned with the species concept, no clear-cut solution within the framework of accepted taxonomic procedure has been possible.

Until 1872, advances in this field had been greatly handicapped by the prevailing notion, purportedly based on unambiguous experimental results, that bacteria exhibit an enormous range of variability. It stands to reason that one can hardly expect to "classify" organisms that behave in the manner claimed for them by the early protagonists of the doctrine of pleomorphism, according to whom practically any bacterium could assume the shape of any other, depending largely on the conditions under which it had developed.

There had been some responsible claims and observations to the contrary. Going back to the pioneering studies of Louis Pasteur, one can find considerable evidence in favor of the view that the transformations claimed by the pleomorphists were, to say the least, not always observed. The experienced eye of the great French chemist-turned-microbiologist, together with his uncanny ability to devise experimental methods apt to give clearly interpretable results, soon convinced him, as they should have convinced others, that there is often a close and consistent correlation between the chemical changes brought about in a particular environment by the organisms growing therein and the microscopic aspects of the cultures. Pasteur had unhesitatingly taken this to mean that there are different and recognizable types among these microorganisms and had proceeded to describe and name them. But some later workers insisted on the occurrence of drastic transformations in the appearance of the organisms themselves with changes in environmental conditions. It was, however, not always appreciated that their observations might equally well be interpreted as resulting from the use of impure cultures, by the mechanism of preferential development of different organisms elicited by modifications of the external milieu. As long as this fundamental ambiguity had not been resolved, the picture remained too confused to permit serious attempts at classification.

It must have been with much relief that bacteriologists who had learned from Lister and Koch how pure cultures could be procured and who had started experimenting with such material became increasingly convinced that the concept of pleomorphism was untenable. Their results clearly indicated that, provided pure cultures, sterile media, and aseptic techniques were employed, transformations of the sort claimed by the pleomorphists simply did not occur. With the gradual development of rigorous techniques and criteria for work with pure cultures, experimental evidence tended more and more to favor the view that even bacteria display a remarkable constancy in both morphological and physiological respects. This further implied the existence of numerous intrinsically different types of bacteria.

At this stage the needs for methods of differentiation and recognition became apparent, and it was Cohn who early made some notable contributions towards filling this need. As one of the leaders in the fight against pleomorphistic dogma, Cohn (1872, p. 133) had raised the question:

> . . . ob es denn bei den Bacterien überhaupt Arten in dem nämlichen Sinne giebt wie bei den höheren Organismen. Selbst wer von der Metamorphosenlehre jener Mykologen nichts wissen will, die Alles aus Allem entstehen und zu Alles sich entwickeln lassen, wird doch beim Anblick eines Bacterienhaufens oft verzweifeln, unter diesen zahlreichen Körperchen von allen möglichen Formen eine Sonderung natürlicher Arten vorzunehmen.

Cohn's conclusion was in the affirmative, as follows from the statement (*ibid.*):

> Gleichwohl bin ich zu der Ueberzeugung gekommen, dass die Bacterien sich in eben so gute und distincte Arten gliedern, wie andere niedere Pflanzen und Thiere, und dass nur ihre ausserordentliche Kleinheit, das meist gesellige Zusammenwohnen verschiedener Species so wie die Variabilität der Arten die Unterscheidung in vielen Fällen für unsere heutigen Mittel unmöglich macht.

In the same paper a beginning was made with the systematic differentiation and naming of bacterial "species." Differentiation was based on morphological characteristics exclusively. This does not mean, however, that Cohn was not aware of the existence of physiological differences as well. He clearly recognized that two morphologically indistinguishable organisms might yet be found to exhibit clear-cut and constant physiological differences. But he found it difficult to determine how far such differences should be accepted as grounds for species differentiation. The pertinent passage in Cohn's paper is, it appears to me, so significant that it is worth quoting in full; a free translation follows. After pointing out that perhaps physiological differences may later be correlated with morphological ones, he stated (*ibid.*, pp. 135–136):

> But, on the other hand, I suspect that in the class of bacteria similar conditions obtain as found in higher animals, and particularly among cultivated plants. Of two almond trees which cannot be distinguished by their growth, their leaves, blossoms, and fruits, not even by the external and microscopic aspects of their seeds, one produces only bitter seeds that contain amygdalin and emulsin and produce toxic hydrocyanic acid, whereas the other always yields sweet almonds. We assume that these two trees belong to the same species and originated from a common ancestor from which the two, physiologically so different, came about through variation. . . . Perhaps there exist also among the bacteria which are morphologically indistinguishable, yet exhibit differences in chemical and physiological activity, similar varieties or races which, initially derived from a common germ, always produce the corresponding products through continued, natural or artificial, cultivation under identical conditions and on the same medium. With various yeast types Rees has demonstrated the formation of special races through artificial cultivation. Just as summer rye is unsuitable for winter seed, though initially both races have the same origin and can be interconverted by prolonged cultivation, so is a top yeast unsuitable for the production of a Bavarian type beer, and nearly every kind of wine or beer is made with its own special yeast. Nonetheless, it is most probable that many alcohol-producing yeasts belong to only one species, comprising numerous "cultured races." I suspect that also among the bacteria, which act as ferments in totally different chemical and pathological processes, there occur, besides a small

number of independent species, a far greater number of natural and "cultivated" races, the latter tenaciously retaining their individual physiological particularities because they multiply exclusively by asexual means.

So keen an appreciation of the value of physiological and biochemical characteristics for systematic purposes inevitably led Cohn to refrain from using them. Nor did this practice cause, at the time, serious inconveniences. In 1872 knowledge of the bacteria was still so rudimentary that the twenty-one species which Cohn proposed satisfactorily consolidated the existing information.

But not for long did this state of sophomoric bliss persist. With the rapidly growing interest in Pasteur's "infiniment petits" as biological agents of economic and particularly sanitary importance, it was only a matter of years before the accumulated information led to the realization that an enormously larger number of "different" bacteria existed, and it thus became necessary to devise more adequate methods for systematizing this knowledge. The approach generally adopted was the creation of a new "species" for every organism that in some respects differed from the previously proposed ones, generally without the least attempt at formulating what was to be understood by a "species" of bacteria. Not until 1912 was this matter clearly discussed by Benecke, and his answer to the question "What is a bacterial species?" was far from reassuring to those who might have felt that it should be possible to establish definite criteria for such entities. With considerable candor Benecke (1912, p. 212) stated: "Die Antwort lautet: Das, was der Forscher, welcher die Art aufstellt, nach seinem 'wissenschaftlichen Takt' darunter zusammenfasst." This statement bears a striking resemblance to Dobzhansky's remembrance of a definition by "an affable systematist": "A species is what a competent systematist considers to be a species." Dobzhansky, however, continued (1941, p. 372):

The cause of this truly amazing situation—a failure to define species which is supposedly one of the basic biological units—is not too difficult to fathom. All of the attempts, mentioned above have striven to accomplish a patently impossible task, namely to produce a definition that would make it possible to decide in any given case whether two given complexes of forms are already separate species or are still only races of a single species. Such a task might be practicable if species were separate acts of creation or arose through single systematic mutations. If species evolve rather than suddenly appear, there will necessarily be a residue of situations intermediate between species and races. This need not, however, deter biologists from attempting to elucidate the nature of species, provided it is clearly realized that no rigid standard of species distinction can be secured.

Even at the time Dobzhansky wrote this passage new concepts had been developed which render the systematic treatment of special groups of higher plants and animals much less arbitrary than the quotations above would seem to imply. Elsewhere in this volume a discussion of such developments may be found; suffice it here to refer to the important contributions by Babcock and Stebbins (1938), Dobzhansky (1941), Petrunkevitch (1952), and Camp (1951). Unfortunately, in the realm of bacteria and bluegreen algae no comparable advances have been made. In large part this is connected with the lack of conclusive evidence for the occurrence of sexual reproduction in these organisms, and Dobzhansky has concisely treated this aspect in the last chapter of his book (1941, p. 379), concluding that "the species as a category which is more fixed and therefore less arbitrary than the rest is lacking in asexual and obligatorily self-fertilizing organisms. All the criteria of species distinction utterly break down in such forms." A similar verdict was rendered earlier by Babcock and Stebbins (1938, p. 64): "The species, in the case of a sexual group, is an actuality as well as a human concept; in an agamic complex it ceases to be an actuality." Even if future investigations were to reveal a more or less common and frequent sexuality in bacteria and bluegreen algae, a phenomenon which at present is suspected to characterize some actinomycetes (Lieske, 1921; Stanier, 1942; Bisset *et al.*, 1951), and perhaps some few strains among the eubacterial groups (Lederberg *et al.*, 1951), the situation hardly warrants the hope that the modern taxonomic concepts of the botanists and zoologists will soon be successfully applied to these microorganisms so as to render the bacterial and myxophycean species "actualities" rather than merely "human concepts."

The arbitrariness of such "species" is now generally conceded. Also, it is well-nigh impossible to escape the conclusion that "scientific tact" in delineating these taxa must carry different connotations for different investigators. This is quite understandable if we realize that it is often imperative, even for no other than strictly practical purposes, to distinguish between individual strains (pure cultures), differing from one another with respect to only one type of property, such as pathogenicity, serological reactions, growth factor requirements, or utilization of special carbohydrates. As has been pointed out in more detail elsewhere (van Niel, 1946) the relative weight given to various possible differential characteristics thus depends to a large extent on the nature of the investigation in which the organisms in question play a role.

In this respect there has been a shift in emphasis in the direction of physiological and biochemical studies. Consequently there has also developed a tendency to use physiological and biochemical criteria for the delineation of species among the bacteria; studies on the physiology of the bluegreen algae have not progressed far enough to include them in the present argument. But this departure from Cohn's approach has rarely been justified, except perhaps on the basis of the consideration that the paucity of morphological characteristics makes it inevitable to resort to the use of differential properties other than morphological ones, and that physiological differences can be regarded as the detectable expressions of differences in submicroscopic morphology (Winslow, 1914; Kluyver and van Niel, 1936). The implications of this procedure have, however, become very clear and very disturbing during the past decade as a result of the important investigations with naturally occurring or artificially induced "mutants" of bacterial cultures. Apart from demonstrating that the properties of a pure culture are not firmly and irrevocably fixed, many of these studies have also indicated that especially the biochemical characteristics of the "mutant strains" show the same sort of relationship to those of the "wild type" as those that have been recognized as the result of single-gene differences in organisms in which the occurrence of sexuality has permitted a genetic analysis. This very fact has sharply raised the question as to how far strains exhibiting such differences should be regarded as distinct species. What Cohn, without benefit of genetic knowledge, had intuitively grasped and clearly expressed, has now once more become a point that has to be seriously analyzed; and it is not an easy problem.

Few taxonomists will challenge the opinion that a series of mutants, produced by the action of mutagenic agents from a pure culture of bacteria, should still be regarded as distinct clones of the same species. But the problem is an altogether different one when the question is transferred to a number of isolates from natural sources showing similar differences. Here the practice has been to indicate such differences by the use of different specific designations. Hence the bacteriological literature is replete with descriptions of "species" that differ no more from one another (as far as the actual characterization has proceeded) than by properties that might well be the result of "single gene" differences. And it should be remarked that it is not only biochemical characters, but also morphological ones that may be affected in a similar manner. The now widely recognized "smooth-rough" variation, determining the appearance of bacterial colonies, may well be a case in point.

In consequence of this situation some students of microbial genetics have expressed the view that the separation of species among the bacteria cannot be taken seriously. And, admittedly, the evidence for the occurrence of variation, even in pure cultures, is so overwhelming that its implications have to be considered. Naively, one might formulate the problem in some such form as: How many differences, equivalent to single-gene differences, shall one accept as justification for the establishment of a species? It will be clear that even this formulation is hardly conducive to a solution of the problem. The geneticist will counter that, by the use of an appropriate methodology, it is easy to produce from a pure culture offspring that differ from it by one-, two-, three-, four-, etc., gene characters. Where, then, shall one draw the line?

The developments sketched in the above paragraphs seem to lead to the conclusion that the problem of speciation in bacteria—and, by a similar reasoning, this would apply equally to the bluegreen algae—has not been solved, and that the recent work on variability and induced mutations has led us back to the stage before Cohn's contributions, when an almost unlimited variability was accepted. Obviously, this new emphasis on variation is not the result of "inadequate techniques"; it is well established, and it is also in much closer agreement with the Darwinian approach to biology. In a sense, one would call Cohn's ideas on classification of bacteria the outcome of the Linnean philosophy; this now has to be abandoned.

It is an interesting problem to consider how far the "evolutionary" approach can ever render service in reaching a more satisfactory basis for establishing some rationale in clarifying the meaning of a bacterial species. Is it really true that we have now to admit that Cohn's predecessors and antagonists have "won," and that an unlimited variability or mutability has to be reckoned with, thus invalidating any and all attempts to arrive at an acceptable concept of a bacterial species? This I do not believe; it will be necessary to recognize, not merely that Cohn's ideas on the constancy of characters was based on inadequate information, but also that his insistence on "constancy" had an equally sound basis in fact. As happens so often in scientific and other controversies, the ultimate answer is not to be found by application of the "either-or" approach, but by synthesis. It is in this respect that the recent contributions of the botanists and zoologists have done so much in bringing about a considerable clarification in problems of "biosystematy," as Camp (1951) calls this branch of science, and the question arises how far similar approaches are possible as a means of reaching the same level with respect to the classification of bacteria and bluegreen algae.

The quotations from Babcock and Dobzhansky show that we cannot expect that the same methods now so successfully used elsewhere will soon solve the problem. But it is important to point out that much can be done, and that a great deal of the present confusion in our thinking is the result of an utterly inadequate appreciation of the truly "biological" possibilities that the bacteria and bluegreen algae still offer. Most of the present difficulties have resulted from studies with isolated, pure cultures, often grown under extremely artificial conditions, having little if anything in common with those that have permitted the persistence of various types of these microbes in nature. No one has realized this fallacy better than Winogradsky who, about thirty years ago, started to inject the notion that pure cultures may be necessary for an adequate study of certain physiological problems, but that an understanding of the role of these organisms in nature cannot be gained exclusively by this methodology (see Winogradsky, 1949). It is from investigations on their behavior in competition with others that we may expect advances which will ultimately be of the greatest significance for gaining a better perspective also concerning the systematics of the organisms. It is quite possible that many of the artificially produced mutants of bacteria can be maintained only under the abnormal conditions provided by the use of pure cultures and culture media that bear no resemblance whatever to the environments in which the organisms are naturally found. For the development of sound principles of bacterial classification it is of the utmost importance that this criticism be heeded; it is a serious one, and suggests at the same time an approach that is far better suited to the problem.

Just as the modern taxonomists of the higher plants and animals have come to insist on the need for far more than the detailed examination of a few museum specimens and have stressed the importance of field studies on naturally occurring populations, amplified by cytological and genetic investigations, bacteriologists must realize that bacterial systematics will not be greatly advanced so long as it remains based largely on routine examination, by standard methods, of pure cultures. In spite of the fact that those pure cultures are "living," they are in some ways not much better than museum specimens; and their continued propagation on the customary nutrient media all too often is apt to induce changes in the organisms which make their recognition as offspring of the initial isolate difficult, if not downright impossible. Numerous are the instances in which a special feature that provided the first impetus to a detailed study of a bacterial culture, be it a characteristic pigmentation, pathogenicity, or biochemical property, such as the ability to live autotrophically as a hydrogen bacterium, or to carry out a vigorous denitrification, was lost on continued cultivation, and the evidence is strong indeed that the use of the routine meat extract-peptone-agar media, on which, to be sure, good growth of the pure culture could be secured, must be held responsible for the changes in characteristics.

It should be self-evident that these remarks are not intended to advocate that pure cultures are useless for taxonomic purposes. Were this implied, the developments would soon lead us back to the pre-Cohn era of experimentation, with results so equivocal that their interpretation would become impossible. No; they are meant to stress the necessity of learning more about the factors that operate in maintaining the various types of bacteria and bluegreen algae in nature. In the elective or enrichment cultures we possess a simple and powerful methodology for achieving this very end. Such cultures permit us to determine which among the vast diversity of germs present in a rich inoculum can successfully compete with the others under the specific environmental conditions, determined and imposed by the investigator, so that gradually they become the predominant microorganisms in the culture. This procedure, chiefly initiated by Beijerinck and Winogradsky (see their *Collected Works,* published in 1921 and 1949, respectively) is pre-eminently suited to determine by direct experiment what particular features of the environment are responsible for the abundant or exclusive development of special types and, by inference, to clarify the "natural" conditions for their existence. Furthermore, the results provide the information necessary for studies on the behavior of pure cultures under such conditions. And last but not least, they can be used to isolate at will from natural sources representatives of those types whose ecological relationships have been sufficiently established. This, in turn, makes it possible to conduct comparative studies with several strains isolated from different localities in order to elucidate the normal range of variation displayed by the "wild types." Amplified with investigations on the competitive value of observed differences in characteristics the accumulated knowledge promises to be far more significant for reaching a satisfactory solution of taxonomic problems than are the results of those "standard tests" which at present are the chief basis of our methods of differentiation, and which are generally performed under conditions and with media utterly at variance with the "natural" ones. (See, in this connection, e. g., van Niel, 1949b; Winogradsky, 1952.)

But however much the approach outlined above may contribute to a better understanding of the microorganisms in question, we should not anticipate that it will solve the "species problem," and this for the reasons already mentioned. Once this is recognized, the question arises whether a more promising attack can be suggested. In this connection I believe that Winogradsky's latest publication (1952) has opened up prospects for sound developments. In essence he proposes the establishment of "biotypes," rather than species, genera, etc., for those groups of bacteria that are easily recognizable and accessible and that represent special and distinctive patterns of characteristics which can be related to the normal role of the organisms in nature. Around these "biotypes" are to be grouped the numerous "satellites," comprising the strains that differ from the "types" only with respect to some secondary details, these to be indicated simply by numbers. Abandoning all attempts at further classification, Winogradsky concludes (1952, pp. 130–131):

> . . . je ne pense pas que ce travail [i.e., to reconstruct present systems of classification along these lines] puisse être entrepris avant longtemps; je crois néanmoins, que mes suggestions se montreront utile du jour où les bactériologistes, fatigués par l'aspect touffu de la systématique bactérienne, songeraient à la réformer en faveur d'un mode plus simple et, à mon avis, plus rationnel.
>
> Il se peut que certains microbiologistes soient choqués par l'idée de supprimer la classification Linnéenne dans le cas des bactéries, habitués qu'ils sont de s'en servir pour toute classification.
>
> Or, tout travail établi selon les règles de cette classification devrait être basé avec quelque précision sur le principe philogénétique, qu'il est impossible d'appliquer aux bactéries. Il serait donc plus correct de nous borner à l'appliquer au règne animal et au règne végétal, òu il est bien à sa place, sans chercher à englober dans sa sphère les formes plus élémentaires de la vie.

On devrait se contenter de ce que les bactéries se laissent tout de même systématiser, sous forme de groupes représentés par des Biotypes, qui sont, eux, bien différenciables.

At first sight this approach may appear simply to avoid the species problem by substituting for it the new one of what shall be considered the criteria for a biotype. Yet this mere substitution may exert a healthy influence because the name is still untinged by connotations such as those that have come to be associated with the term "species." Also in connection with the problems to be discussed in the next section, acceptance of Winogradsky's proposal would go far in removing obstacles that must otherwise be faced.

The validity of these statements is well illustrated by the following example. It can be reasonably expected that some of the "biotypes" established in the course of time would correspond more or less closely with now accepted "true species" of bacteria. The use of the latter term has, however, been restricted and is generally applicable only to the first described species of a genus, a situation that results from the virtually complete acceptance by bacterial systematists of the rules of nomenclature adopted by the botanists. Now, this inevitably entails the consequence that a number of "type species" represent bacteria that have not been studied in sufficient detail to make them acceptable as biotypes in the sense in which I have interpreted this expression in the preceding pages, and which would definitely include the availability of specific elective culture procedures for the organism in question. Adherence to the present code of bacterial nomenclature would make it difficult to change a large number of "type species"; but when "biotype" is used instead, no one is hampered by "rules and regulations" that have not yet been formulated.

Winogradsky's suggestions therefore appear to me worthy of careful consideration and strong support; in a sense they represent a logical development of my own ideas, expressed some years ago as follows (van Niel, 1946, pp. 297–298):

Discontinuation of the terms species and genus for bacteria, along with the introduction of multiple keys, would eliminate some of the difficulties now encountered, because it would insure a far greater autonomy to specialists in dealing with their own groups and problems, unencumbered by the exigencies of different groups. There would be no need for the sort of consistency required as the foundation of a single system of classification. Whether the further elaboration of a rational nomenclature along the lines laid down by Orla-Jensen, and further expanded by Kluyver and van Niel, would prove adequate, or whether it might even be preferable to drop the use of Latin names with their taxonomic implications, is a matter for future developments. And, while I am fully in agreement with the opinion that stability in nomenclature is of great importance, I must once more insist that, in the long run, it may turn out to be easier to gain adherence to a more rational, modernized system than to the current one.

The Genera, Families, and Orders of the Bacteria and Bluegreen Algae

In the development of our system of classification the discovery and naming of species with a generic and specific name came first. Grouping into Genera was followed by grouping of Genera into Tribes and Tribes into Families and Families into Orders. In developing the key in the reverse order, the authors of the keys in the Manual were forced to use initially for identification characters which by their very nature are largely indeterminable.—V. B. D. Skerman, 1949, pp. 177–178.

What made Winogradsky (1952) grant that the systematics of plants and animals on the basis of the Linnean system is defensible, while contending that a similar classification of the bacteria is out of the question? The answer must be obvious to those who recognize in the former an increasingly successful attempt at reconstructing a phylogenetic history of the higher plants and animals, based on comparative-anatomical, embryological, distributional, ecological, and paleontological studies and who feel that comparable efforts in the realm of the bacteria (and bluegreen algae) are doomed to failure because it does not appear likely that criteria of truly phylogenetic significance can be devised for these organisms. Forty-five years ago Orla-Jensen (1909) believed that it was possible to formulate an acceptable phylogeny of the bacteria by means of physiological-biochemical considerations. But it has since been shown that there are compelling reasons for doubting the validity of Orla-Jensen's premises (Oparin, 1938; van Niel, 1946; 1949a).

Nevertheless, systems of classification of these organisms, complete with genera, families, and orders have been developed in the course of the past century; they have become more and more elaborate and complicated, and seem to be taken seriously in at least some quarters. The simplest explanation for this attitude is that classifying organisms in this manner has become an accepted habit, so ingrained that one just kept on doing it, to paraphrase the last verse of Paul Géraldy's "Méditation"[1]:

> On prend l'habitude, vite,
> d'échanger de petits mots.
>
> Quand on a longtemps dit les mêmes,
> on les redit sans y penser.
> Et alors, mon Dieu, l'on aime
> parce qu'on a commencé.

When Cohn (1872) first proposed his six bacterial genera he was, however, quite explicit in stating that these units did not have any phylogenetic significance. They were simply "form-genera," providing descriptive names for groups of bacteria possessing similar shapes. Though useless as guides to "natural relationships," these categories greatly facilitated the naming and identification of bacteria. Once a newly isolated culture had been characterized as composed of short rods, for example, it was thereby fixed as a *Bacterium* species, and the establishment of its possible identity with earlier described bacteria could be restricted to a comparison with the known members of this genus.

Cohn subsequently (1875) expanded his system considerably, integrating the (form-)genera of the bluegreen algae with those of the bacteria as components of the class or family of the Schizomycetes. With further increase in our knowledge of these microorganisms, owing largely to advances in microscopic techniques, additional differential properties were discovered. Incorporation of such characteristics in the descriptions consequently led to modifications of the diagnosis of several genera, and to the proposal of many new ones. During this period a number of more or less "private" systems of classification were developed, such as those of Zopf, Marpmann, de Bary, Fischer, Lehmann and Neumann, Migula, Kruse, Orla-Jensen, and Chester, each one commanding a certain number of adherents, with the result that various authors might refer to one and the same organism by several different names. An extensive study of this somewhat con-

1. Paul Géraldy, *Toi et Moi*, Paris: Stock, 1922.

fusing situation was made by a Committee of the Society of American Bacteriologists whose members published reports and recommendations (Winslow *et al.*, 1917, 1920) for the development of a more uniform system of classification of the bacteria, largely based on Buchanan's proposals (1916–1918). This became the nucleus from which originated in due course *Bergey's Manual of Determinative Bacteriology* (1923–1948), prepared by an ever-increasing number of specialists with expert knowledge of various groups of bacteria (Breed *et al.*, 1948). The classification followed in this handbook has been more and more generally adopted and is today the most widely used.

But in spite of the growing recognition afforded the painstaking efforts represented by this collaborative enterprise, the end result has never been wholly satisfactory, and each successive edition has come in for a certain amount of criticism. Objections have been raised to the inclusion of a vast array of poorly characterized species, for example by Winogradsky (1952) and Skerman, the latter presenting a well-reasoned argument (Skerman, 1949, p. 175):

> Many of the descriptions of bacteria in Bergey's *Manual of Determinative Bacteriology* are decidedly poor when viewed from present-day standards. Some will be difficult to improve since a number of the original cultures have probably been lost. The original descriptions which still remain on record present us with an awkward problem in establishing priorities. Some of these descriptions are so inadequate that one description could be equally well applied to many new isolates. The original authors cannot be blamed for the inadequacy of these descriptions which no doubt conformed to the standard of the day and it would be a breach of ethics to refuse recognition of these descriptions. Nevertheless present-day workers cannot regain the original cultures in some instances to subject them to further examination and would-be key formers are handicapped by the lack of this information. Thus one cause of the chaotic state of bacterial nomenclature is the lack of "type" specimens regarded as essential by systematic botanists. There is only one remedy for this, namely the redescription of all available cultures according to a certain code which should be applied to all bacteria alike. On the basis of these descriptions the organisms should be renamed, for the most part with the names they now possess. Priorities should be based on these names and all descriptions and names for which there are no procurable cultures should, by common consent, be discarded.

Besides, the characterization of many of the genera has been found wanting, and again I quote from Skerman (1949, p. 176):

> There is also need for more precise definitions for genera. In the hands of the authors of most of our textbooks the term "definition" has entirely lost its meaning. Many of the definitions contain very little which is definite. They approach more towards condensed, and often confusing, descriptions which attempt to embrace all the possibilities which one may encounter among the species in the genus rather than a precise statement of the characters which can be uniformly found among all or the majority of species within that genus to be distinguished from other genera.

And finally the taxa of higher order suffer from the same deficiency, here even more aggravated because, as Skerman remarks (*ibid.*, p. 177):

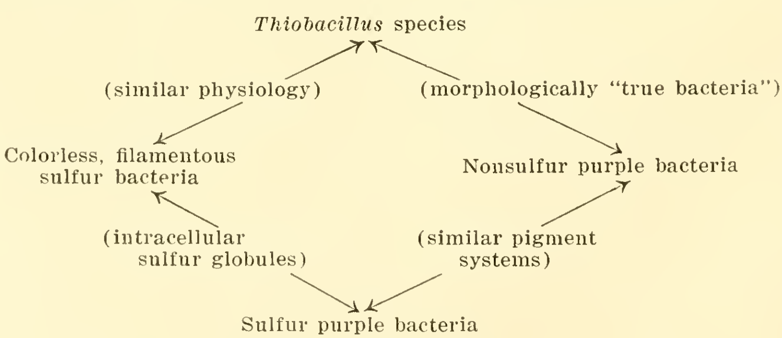
> A close study of the number of determinable characters which could represent all species within a genus would reveal this number to be very small. The number of characters which are common to all genera within a tribe must inevitably be smaller, and would continue to diminish as groupings become broader.

These remarks should suffice to indicate that the satisfactory demarcation of systematic units above the rank of species is beset with even greater difficulties than that concerned with mere species. Occasionally, however, a particular property has been encountered which is qualitatively so striking that it would appear suitable as the special distinguishing character of a family or order. This happened, for example, when Migula (1897) introduced the order Thiobacteria for those microbes which Winogradsky had called "sulfur bacteria." It was the first time that the bacteria were divided into two separate orders; and Migula justified the procedure by emphasizing that both the cellular organization and the physiology of the sulfur bacteria were clearly distinct from those of the "true" bacteria, or Eubacteria.[2] Morphologically the former are conspicuous on account of their relatively large size and their content of sulfur globules; physiologically they represent the prototype of the autotrophic bacteria; they can grow in strictly mineral media, and are dependent on an external supply of sulfide which is oxidized to sulfate.

It was also the first time that a physiological property was used for the establishment of a large systematic group of the bacteria. Coupled as it was in this case with some morphological peculiarities, this may have appeared defensible. But later developments have shown how much confusion was created by this ostensibly simple expedient.

Elsewhere I have sketched these developments in some detail (van Niel, 1944); suffice it here to recapitulate the major aspects. The Thiobacteria, in 1900, comprised two subgroups, viz., the colorless, filamentous organisms which, except for lack of pigmentation, closely resemble the bluegreen algae of the family Oscillatoriaceae (see, e.g., Pringsheim, 1949), and the red-colored, so-called purple sulfur bacteria which are much more "bacteria-like," though generally much larger. Within a decade, however, two more groups of organisms were discovered with characteristics that made their incorporation into one or the other of Migula's orders largely a matter of personal preference. These were the small, colorless *Thiobacillus* species, physiologically typical sulfur bacteria, but morphologically in no way distinguishable from many eubacterial types, and the small purple bacteria that are physiologically not sulfur bacteria, though their pigment system, composed of chlorophyllous and carotenoid components, closely resembles that of the purple sulfur bacteria.

The properties of these four groups obviously show "interrelationships" which can best be presented in the form of a diagram, as follows:



2. In an earlier publication (van Niel, 1944) I erroneously stated: "One looks in vain, however, for an exposition of the reasons which had induced Migula to create the new orders" (p. 71). A vague attempt at rationalizing this measure can be found in the brief section on the sulfur bacteria at the end of Vol. 1 of Migula's *System*.

This diagram shows that the new situation called for a decision as to the relative importance of the characters that can be used to link the different groups. Obviously, a combination of morphological and physiological properties, once justified because "intermediate" groups were not known, was no longer adequate. The formulation of a diagnosis of separate orders had, from now on, to be based on either morphological or physiological features. Even this could not provide a fully satisfactory solution to the problem of establishing larger systematic units, however. For, when "morphology" was given preference, there would still be the question whether the occurrence of sulfur globules, the individual cell size, or the presence or absence of the special pigment system was considered the most significant, while preferential use of physiological characters would imply the need for "grading" the respective values of sulfide oxidation and pigment formation.

Of course, the very admission of physiological characters in bacterial systematics might be blamed for the confused situation here discussed. Would it not have been better if such criteria had been left out altogether in the creation of the two orders? In that event the filamentous colorless sulfur bacteria could have been neatly segregated from the *Thiobacillus* group and from the sulfur and nonsulfur purple bacteria, regarding the latter assemblage as members of the order Eubacteriales. While this may be considered a great improvement, it nevertheless serves merely to shift the basic problem to the question of how families should be defined. It can still be maintained that there would be ample justification for the creation of a large systematic group of all the purple bacteria, especially because it is now known that the pigment system of these organisms confers upon them the ability to carry out an "aberrant" photosynthetic mode of life (Molisch, 1907; Buder, 1919; van Niel, 1931, 1941, 1952). And many arguments could be advanced to defend the thesis that such a unit, which would also accommodate the green sulfur bacteria, has considerably greater phylogenetic significance than, for example, groups comprising all Gram negative, nonsporeforming, polarly flagellated rod-shaped bacteria, regardless of their physiological properties.

The preceding discussion of the systematic status of the sulfur- and purple bacteria may have served to illustrate the difficulties inherent in attempts to accomplish primary divisions in the realm of the bacteria. Similar difficulties are encountered at lower levels, and here, too, the problem must be faced whether physiological characters are admissible. In some circles the idea that they are not still prevails; on the other hand, the large number of generic names with definite physiological connotations (*Thiobacillus, Acetobacter, Lactobacillus, Propionibacterium, Hydrogenomonas, Nitrobacter, Methanococcus, Photobacterium,* etc.) testifies that this attitude is not universal.

Many of these names were introduced by Beijerinck and Winogradsky, and it is clear that the ecological-physiological approach to general microbiology of these two masters was largely responsible for the practice. The discovery that a particular type of metabolism (sulfur oxidation, acetic acid production, lactic or propionic acid formation, hydrogen or nitrite oxidation, methane production, or ability to luminesce) seemed to be closely associated with certain types of bacteria that were both easily procurable and readily distinguishable, comprising relatively small groups of organisms with many common morphological characteristics in each group, naturally suggested the existence of a high degree of specificity which was reflected in both physiological and morphological properties. Since each group contained representatives exhibiting minor differences, one from the other, in shape, size, color, or physiology, it must have seemed eminently rational to consider these as species and the entire group as a genus. A logical consequence of this approach was Orla-Jensen's classification (1909) in which the bacteria were assigned to genera that were defined by a combination of morphological and physiological characters. By considerably extending the number of differential morphological traits and incorporating the newer concepts of the mechanisms of biochemical processes, derived from studies on the comparative biochemistry of microorganisms, Kluyver and van Niel (1936) sought to provide a more up-to-date system along the same general lines.

Some systematists have, however, consistently condemned the use of physiological criteria for the definition of even such small taxonomic units as genera. They seem to agree with Lehmann and Neumann (1927, 2:190) who wrote:

> Dass die Systematik der Spaltpilze und der ihnen nahestehenden Mikroorganismen genau so wie die aller anderen Lebewesen zunächst nach morphologischen Grundsätzen (Form, Begeisselung, Sporenbildung) versucht werden muss, ist klar, trotz aller oben angegebenen Schwierigkeiten.

Statements to this effect can be found, for example, in Prévot's extensive paper on the classification of the anaerobic cocci (1939, p. 50):

> . . . nous pensions qu'il est possible aujourd'hui de chercher à adapter au monde bactérien les doctrines classiques qui ont réuissi pour le règne végétal et le règne animal entre les mains des frères de Jussieu, de Cuvier, de Geoffroy Saint-Hilaire, etc., et des modernes: il existe une relation entre la valeur des charactères et le déterminisme du groupement des Bactéries, et cette relation est commune au trois mondes, végétal, animal et bactérien: les charactères morphologiques ont la priorité sur les charactères physiologiques.

On the basis of such considerations Prévot has even developed a set of rules for the delineation of taxa of higher order, as follows (*ibid.*, p. 61):

> Les charactères de morphologie générale sont des charactères de classe.
>
> Les charactères de reproduction (simple, par spore, par conidie) sont des charactères d'ordre.
>
> Les charactères de structure cytochimique (coloration de Gram) sont des charactères de famille.
>
> Les charactères de morphologie spéciale (ectoplasme, biométrie, directions de division, arrangement cellulaire) sont des charactères de genre.
>
> Les charactères physiologiques (culturaux, pathogènes, biochemiques) sont des charactères d'espèce.
>
> Les charactères physiologiques secondaires et sérologiques (agglutination) sont des charactères de variété ou race.

From a scientific viewpoint it is, however, astonishing that the validity of such verdicts generally seems to have been taken for granted; rarely, if ever, has an attempt been made to justify the belief that for the purpose of classification of the bacteria morphological characters are more significant than physiological or biochemical properties. Occasionally it is possible to infer from the context the reasons for this notion. The reference to Jussieu, Cuvier, and Saint-Hilaire in the above quotation from Prévost, for example, indicates the trend of thought. And Kluyver and van Niel (1936, p. 370) expressed this still more directly:

. . . It cannot be denied that the studies in comparative morphology made by botanists and zoologists have made phylogeny a reality. Under these circumstances it seems appropriate to accept the phylogenetic principle also in bacterial classification.

The question then arises in what characters phylogeny expresses itself. There is no doubt that in this respect morphology remains the first and most reliable guide.

But is this inference concerning the superior value of morphological properties actually applicable to the bacteria and bluegreen algae? It has been used to justify the establishment of taxa above the rank of species for organisms with similar outward shape, and the tacit implication has been that such taxa reflect truly "natural relationships." This, however, is open to serious doubt, as illustrated by the genus *Sarcina,* comprising bacteria of spherical shape, dividing in two or three perpendicular directions, thus producing squares, flat sheets, or cubical packages. It would not be surprising to find that bacteriologists familiar with these organisms balk at the notion that the aerobic *S. lutea,* the anaerobic *S. ventriculi, S. maxima,* and *S. methanica,* exhibiting an alcoholic, butyric acid, and methane fermentation, respectively, the halophilic *S. gigantea,* and the motile, sporeforming *S. ureae* represent a group of phylogenetically closely related types.

It seems to me that the most important reason for much confused thinking about bacterial classification is that Cohn's careful appraisal of the meaning of his "form genera" has not been given the attention it deserves. Proponents of the view that morphological characters are of primary importance for the establishment of natural relations appear often to have failed to realize that only those associated with the developmental history or embryology of a higher plant or animal have served to trace its phylogeny. Even though a sufficiently advanced knowledge of the various types of organisms may sometimes permit the use of a special shape as the only character needed for the determination of relationships, this approach can be very precarious, as shown, for example by *Ginkgo biloba* and the whales. Now, most bacteria and bluegreen algae do not exhibit the kind of developmental history that can be useful in reconstructing phylogeny. Once this is recognized, genera such as *Sarcina* stand revealed as signifying no more than the "form genera" of Cohn.

It should thus be evident that many of the morphological features used in the past as differential characters in the classification of bacteria and bluegreen algae cannot be depended upon as guides to phylogeny. Is there any reason to believe that physiological and biochemical properties are more significant in this respect? A priori this possibility cannot be dismissed; there does not seem to be any valid basis for Prévot's insistence that these can be used only for the differentiation of species but not of higher taxa. In fact, the group of photosynthetic bacteria (green and purple sulfur bacteria, and nonsulfur purple and brown bacteria), as also that of the lactic acid bacteria in the sense of Orla-Jensen can easily be regarded as phylogenetically much more homogeneous than the *Sarcina* group, in spite of a considerably diversified morphology among the organisms comprising the first two assemblages. In the photosynthetic bacteria the cell shapes range from small spheres and short rods to large vibrios, rods, and spirals, and the lactic acid bacteria include streptococci, tetracocci, short rods, and long rods, even to the point of becoming filamentous.

But, while discrediting Prévot's contention, this argument does not mean that a particular type of metabolism is a more reliable index of phylogeny than is the gross morphology of the cells. The ability to carry out a lactic acid fermentation, for example, is not the prerogative of the "lactic acid bacteria"; it has been found also in some members of the facultatively anaerobic sporeformers. Similarly, a typical alcoholic fermentation is produced by *Sarcina ventriculi* and by *Pseudomonas lindneri*, and a propionic acid fermentation by *Propionibacterium* species as well as by some anaerobic micrococci, anaerobic sporeformers, and facultatively anaerobic myxobacteria of the *Cytophaga* type. In these cases it is as difficult to find convincing grounds for the claim that the organisms characterized by similarity in metabolism are phylogenetically closely related as it is to assign natural relationships primarily on the basis of cell shapes.

Awareness of this situation led Kluyver and van Niel (1936) to propose that a bacterial genus be defined both morphologically and biochemically. In this manner cross-relations in these two respects could find adequate expression, and homogeneity in the composition of the individual genera was insured. However, it did not solve the problem of a phylogenetic classification; once more it was necessary to make a choice between morphological and physiological characters, now for delineating families, and from the foregoing discussion it would appear that a decision in this respect had to be an arbitrary one.

Besides, another difficulty presents itself, even on the genus level, because not all biochemical properties appeared equally suitable as generic characters. In some cases a guiding principle can be found to aid in evaluating various features. Thus, the lactic acid fermentation brought about by the lactic acid bacteria, the mixed acid fermentation of *Escherichia coli* and its relatives, the ethanol-butanediol fermentation of *Aerobacter* and *Aerobacillus*, the propionic acid fermentation, the butanol-acetone fermentation, the ethanol-acetone fermentation of *Bacillus macerans*, the alcoholic fermentation of *Sarcina ventriculi* and *Pseudomonas lindneri*, represent as many distinctive metabolic patterns. It was therefore felt that they provide legitimate criteria for separate biochemical genera, while the differential utilization of some particular members of the class of carbohydrates, presumably depending merely on the presence or absence of specific carbohydrases, was deemed useful only for the demarcation of species. There are, however, many instances in which the situation is more complicated because one and the same bacterium may exhibit a number of different metabolic patterns, each one of which would be suitable for the definition of a "biochemical genus." This again implies the need for making a choice. As a way out of the dilemma Kluyver and van Niel (1936, p. 389) suggested:

> . . . In those cases it is, of course, desirable to classify the organism in question according to its most characteristic type of katabolism, that is, the type which permits the distinction from otherwise related organisms. This implies that for organisms capable of development under anaerobic conditions the katabolic process involved in this mode of life has been determinative, regardless of the question whether or not the organism also possesses a respiratory mechanism. If two different types of anaerobic katabolism, e.g., saccharolytic and proteolytic, are represesnted, the latter, as being the rarer, has been decisive.

It will be superfluous to belabor the point that this passage contains nothing to suggest a phylogenetic basis for the choice, nor does it seem likely that a sound one can be discovered. Nevertheless, the classification proposed has much to recommend it, because it permits the ready assignment of a particular bacterium to a specific and small group as soon as its general morphological and biochemical characters are known. Final identification then requires comparison with other members of only this assemblage. The advantage is, therefore, of the same kind as that offered by Cohn's "form genera," and the categories resulting from the combination of morphological and biochemical properties are, in a sense, quite comparable though more numerous. In view of the great increase in the number of different types of bacteria discovered in the course of time this is a distinct benefit. Undoubtedly, such strictly utilitarian considerations were responsible for the application of biochemical criteria in the manner outlined above, as shown especially by the decision to use the "rarer" of two otherwise equivalent characters.

But if the homogeneous, morphologically and biochemically defined genera cannot lay claim to phylogenetic significance, the superstructures of tribes, families, and orders can do so even less. It follows that the existing systems of classification of the bacteria and bluegreen algae should not be considered "natural" ones. If this be granted, the question whether retention of such systems is advisable can be examined more critically.

At first sight the now more or less generally accepted genera and families of these organisms, even if devoid of phylogenetic meaning, might appear to serve as a fully satisfactory framework for purely determinative purposes. This, however, can be contested on the ground that they are too rigid, because the families, tribes, and orders represent collections of genera grouped together on the basis of only one set of arbitrarily chosen "primary" characters. While these may be the most useful ones as determinative aids in some instances, in others a different set of primary divisions would be preferable, thereby yielding a superstructure of different composition. It is obviously inadmissible to include a particular "genus" in two or more different families, tribes, or orders. But if these larger groups are considered as no more than convenient contrivances for rapid identification, there is no need to insist on an "either-or" approach. By discontinuing the use of families, tribes, and orders it becomes possible to construct a diversity of groupings in which all the different opportunities for emphasizing similarities in various respects can be expressed. It seems to me a dubious gain to have all the photosynthetic bacteria assembled in a suborder, Rhodobacteriineae, if this practice eliminates the possibility of recognizing the existence of the large group of "sulfur bacteria" comprising only some of the photosynthetic bacteria in addition to organisms now incorporated in the orders Eubacteriales (genus *Thiobacillus*) and Chlamydobacteriales (families Beggiatoaceae and Achromatiaceae). Such an entity as the sulfur bacteria remains an extremely useful assemblage, since it represents an ecological-physiological community of all the conspicuous inhabitants of natural environments in which hydrogen sulfide is present.

It is not hereby intended to dispute the probability that the photosynthetic bacteria actually represent a phylogenetically related group, nor that the Beggiatoaceae might be similarly regarded. But the phylogenetic relationships of the other "sulfur bacteria" are far less certain. Clearly, it is not imperative that even the probable affinities of the first-mentioned organisms be given recognition by uniting them into a family, tribe, suborder, or order; and if doing so implies that bacteria with doubtful phylogeny must then be treated likewise, there seems to be much in favor of abandoning the practice. If and when the natural relationships of a large number of bacteria have been unambiguously established, it would become advisable to consider the construction of a system of classification based on phylogeny.

As long as this remains a pious hope for the future, one might do well to approach the problem of the classification of bacteria and bluegreen algae in the manner suggested by Winogradsky's latest recommendations. Substitution of "biotypes" for genera and species, and the use of common names, such as "sulfur bacteria," "photosynthetic bacteria," "chemoautotrophic bacteria," "denitrifying bacteria," "nitrogen-fixing bacteria," etc., instead of the Latin names representing taxonomic units with definite phylogenetic implications, would permit the development of more rational arrangements for the rapid identification and comparison of the organisms. This problem calls for an elaborate system of cross-indexing of their properties, and the present organization, based on the Linnean approach, not only is unjustifiably pretentious, but also impedes the best utilization of established characteristics because they are employed for the construction of mutually exclusive combinations. While much can be done to remedy the resulting situation through the preparation of mechanical keys, such as the eminently useful one developed by Skerman (1949), a more radical departure from accepted procedure remains desirable in the opinion of the writer.

In this connection attention should be called to the ideas recently expressed by C. H. Andrewes concerning the classification and nomenclature of viruses (1952, p. 136):

> The nomenclature of plants and animals has been the subject of much controversy and change, owing largely to the fact that the earlier names were bestowed without understanding of the principles of taxonomy as we now know it, often without reference to type material, and on the basis of very inadequate descriptions. In the reviewer's opinion, such troubles would be avoided in the virus field by dating valid nomenclature in this group not from the time of Linnaeus 200 years ago, but from a date to be decided upon in the future. . . .
>
> A very few descriptions of viruses published hitherto would satisfy those who are seriously considering the matter today. Binomials are not in common use for any viruses, and there seems therefore everything to be gained by starting with a clean sheet. . . . Such virus names already published as seem suitable would also be validated, but virus nomenclature need not be forever overlaid by the dead hand of bad naming, linked to descriptions which are hard to interpret and are based on unsuitable guiding principles. If, however, students of viruses take thought in time and base their classification and nomenclature on solid foundations with reference from the very beginning to type material, they can forever be free from the nightmares of change and contentiousness which bedevil nomenclature in other fields.

In contrast to the quotation at the start of this paper, the above, with a few minor modifications, seems eminently applicable to the problems presented by the classification of the bacteria and bluegreen algae.

REFERENCES

Andrewes, C. H.

1952. Classification and nomenclature of viruses. Ann. Rev. Microbiol., 6:119–138.

Andrewes, F. W.

1930. The nomenclature and classification of micro-organisms. *In* A System of Bacteriology, 1:292–310. London: Med. Res. Council.

Babcock, E. B. and G. L. Stebbins, Jr.

1938. The American Species of *Crepis*. Carnegie Inst. Washington Publ. 504. 199 pp. Washington.

Badian, J.

1933. Eine cytologische Untersuchung über das Chromatin und den Entwicklungszyclus der Bakterien. Arch. Mikrobiol., 4:409–418.

Beijerinck, M. W.

1921. Verzamelde Geschriften. Vols. I–V. The Hague: M. Nyhoff.

Benecke, W.

1912. Bau und Leben der Bakterien. xii + 650 pp. Leipzig: Teubner.

Bissett, K. A., J. Greene, and E. O. Morris

1951. The nuclear reduction process in bacteria. Exp. Cell. Res., 2:388–392.

Boivin, A.

1948. Les acides nucléiques dans la constitution cytologique et dans la vie de la cellule bactérienne. Compt. Rend. Soc. Biol., 142:1258–1275.

Breed, R. S., E. G. D. Murray, and A. P. Hitchens, eds.

1948. Bergey's Manual of Determinative Bacteriology. 6th ed. xvi + 1529 pp. Baltimore: Williams and Wilkins Co.

Buchanan, R. E.

1916–1918. Studies in the nomenclature and classification of the bacteria. I–X. Journ. Bact., 1(1916):591–596; 2(1917):155–162, 347–350, 603–617; 3(1918): 27–61, 175–181, 301–306, 403–406, 461–474, 541–545.

1925. General Systematic Bacteriology. 597 pp. Baltimore: Williams and Wilkins Co.

Buder, J.

1919. Zur Biologie des Bakteriopurpurins und der Purpurbakterien. Jahrb. Wiss. Bot., 58:525–628.

Bütschli, O.

1889. Protozoa. *In* H. G. Bronn's Klassen und Ordnungen des Thier-Reichs. Vols. I–III. Leipzig and Heidelberg: C. F. Winter.

Calvin, M., and V. Lynch

1952. Grana-like structures of *Synechococcus cedorum*. Nature, 16g:455–456.

Camp, W. H.

1951. Biosystematy. Brittonia, 7:113–127.

Camp, W. H., and C. L. Gilly

1943. The structure and origin of species. Brittonia, 4:323–385.

Cohn, F.

1854. Untersuchungen über die Entwicklungsgeschichte der mikroskopischen Algen und Pilze. Nov. Act. Leo.-Carol., 24:103–256.

1872. Untersuchungen über Bacterien. Beitr. Biol. Pflanz., Heft 2, pp. 127–224.

1875. Untersuchungen über Bacterien. II. Beitr. Biol. Pflanz., Heft 3, pp. 141–208.

Copeland, H. F.

1938. The kingdoms of organisms. Quart. Rev. Biol., 13:383–420.

1947. Progress report on basic classification. Amer. Nat. 81:340–350.

DeLamater, E. D.

1952. Preliminary observations on the occurrence of a typical mitotic process in micrococci. Bull. Torrey Club, 79:1–5.

DeLamater, E. D. (Cont.)

1952. Evidence for the occurrence of true mitosis in bacteria and certain applications. Journ. Invest. Dermatol., 18:225–230.

Delaporte, B.

1939. Recherches cytologiques sur les Bactéries et les Cyanophycées. 160 pp. Paris: André Lesot.

Dobzhansky, T.

1941. Genetics and the Origin of Species. xiii + 446 pp. New York: Columbia Univ. Press.

Enderlein, G.

1925. Bakterien-Cyclogenie. 390 pp. Berlin and Leipzig: De Gruyter & Co.

Geitler, L.

1932. Cyanophyceae. *In* L. Rabenhorst, Kryptogamen-Flora von Deutschland, österreich und der Schweiz. 2d ed. Vol. XIV. 1196 pp.

Gilmour, J. S. L.

1951. The development of taxonomic theory since 1851. Nature: 168:400–402.

Haeckel, E.

1866. Generelle Morphologie der Organismen. Bd. I. Allgemeine Anatomie der Organismen. xxxii + 574 pp. Bd. II. Allgemeine Entwickelungsgeschichte der Organismen. clx + 462 pp. Berlin: Georg Reimer.

Hayes, W.

1952. Recombination in *Bact. coli* K12. Unidirectional transfer of genetic material. Nature, 169:118–119.

1952. Genetic recombination in *Bact. coli* K12. Analysis of the stimulating effect of ultraviolet light. Nature, 169:1017–1018.

Kent, W. Saville

1880–1882. A Manual of the Infusoria. Vols. I-III. London: David Bogue.

Kluyver, A. J. and C. B. van Niel

1936. Prospects for a natural system of classification of bacteria. Centr. Bakt., II. Abt., 94:369–403.

Knaysi, G.

1951. The structure of the bacterial cell. *In* C. H. Werkman and P. W. Wilson, eds.; Bacterial Physiology, espec. pp. 31–37. New York: Acad. Press.

Knaysi, G., and R. F. Baker

1947. Demonstration with electron microscope of a nucleus in *Bacillus mycoides* grown in a nitrogen-free medium. Journ. Bact., 54:4–5.

Lederberg, J.

1947. Gene recombination and linked segregations in *Escherichia coli.* Genetics, 32:505–525.

Lederberg, J., E. M. Lederberg, N. D. Zinder, and E. R. Lively

1951. Recombination analysis of bacterial heredity. Cold Spring Harbor Symp., 16:413–443.

Lederberg, J., and E. L. Tatum

1946. Novel genotypes in mixed cultures of biochemical mutants of bacteria. Cold Spring Harbor Symp., 11:113–114.

Lehmann, K. B., and R. O. Neumann

1926–1927. Bakteriologie, insbesondere bakteriologische Diagnostik. 7th ed. Vols. I–II. Münich: J. F. Lehmann.

Lieske, R.

1921. Morphologie und Biologie der Strahlenpilze (Actinomyceten). ix + 292 pp. Leipzig: Bornträger.

Migula, W.

1897–1900. System der Bakterien. Vols. I–II. Jena: G. Fischer.

1907. Allgemeine Morphologie, Entwicklungsgeschichte, Anatomie und Systematik der Schizomyceten. *In* Lafar's Handbuch der technischen Mykologie, 1:29–149. Jena: G. Fischer.

Molisch, H.

1907. Die Purpurbakterien nach neuen Untersuchungen. vii + 95 pp. Jena: G. Fischer.

Nägeli, C. W. von

1857. Bericht über die Verhandlungen der botanischen Section der 33. Versammlung deutscher Naturforscher und Aertzte. Bot. Zeit., 15:760–761.

Niel, C. B. van

1931. On the morphology and physiology of the purple and green sulphur bacteria. Arch. Mikrobiol., 3:1–112.

1941. The bacterial photosyntheses and their importance for the general problem of photosynthesis. Advances in Enzymology, 1:263–328.

1944. The culture, general physiology, morphology, and classification of the non-sulfur purple and brown bacteria. Bact. Rev., 8:1–118.

1946. The classification and natural relationships of bacteria. Cold Spring Harbor Symp., 11:285–301.

1949a. The comparative biochemistry of photosynthesis. *In* J. Franck and W. Loomis, eds., Photosynthesis of Plants, pp. 437–495. Ames, Iowa: Iowa State Coll. Press.

1949b. The "Delft School" and the rise of general microbiology. Bact. Rev., 13: 161–174.

1952. Bacterial Photosyntheses. *In* J. B. Sumner and K. Myrbäck, eds., "The Enzymes," II:1074–1088. New York: Acad. Press.

Oparin, A. I.

1938. The Origin of Life. (Transl. by S. Morgulis.) 270 pp. New York. Macmillan Co.

Orla-Jensen, S.

1909. Die Hauptlinien des natürlichen Bakteriensystems. Centr. Bakt., Abt. II. 22:305–346.

Petrunkevitch, A.

1952. Macroevolution and the fossil record of Arachnida. Amer. Scient., 40:99–122.

Piekarski, G.

1937. Cytologische Untersuchungen an Paratyphus- und Colibakterien. Arch. Mikrobiol., 8:428–439.

Potthoff, H.

1922. Zur Entwicklungsgeschichte der Gattungen *Chromatium* und *Spirillum*. Centr. Bakt., Abt. II, 55:9–13.

1924. Zur Entwicklungsgeschichte der Bakteriengattungen *Chromatium*, *Spirillum* und *Pseudomonas*. Centr. Bakt., Abt. II, 61:249–255.

Prévot, A. R.

1933. Études de systématique bactérienne. Ann. Sci. Nat. Bot., ser. 10, 15:23–260.

1940. Manuel de classification et de détermination des bactéries anaérobies. 223 pp. Paris: Masson et Cie.

PRINGSHEIM, E. G.

1949. The relationship between bacteria and Myxophyceae. Bact. Rev., 13:47–98.

ROBINOW, C. F.

1944. Cytological observations on *Bact. coli*, *Proteus vulgaris*, and various aerobic spore-forming bacteria with special reference to the nuclear structures. Journ. Hyg., 43:413–423.

1945. Nuclear apparatus and cell structure of rod-shaped bacteria. *In* R. J. Dubos, The Bacterial Cell, "Addendum," pp. 355–377. Cambridge: Harvard Univ. Press.

SCHACHMAN, H. K., A. B. PARDEE, and R. Y. STANIER

1952. Studies on the macromolecular organization of microbial cells. Arch. Biochem. and Biophys., 38:245–260.

SKERMAN, V. B. D.

1949. A mechanical key for the generic identification of bacteria. Bact. Rev., 13:175–188.

STANIER, R. Y.

1942. Agar-decomposing strains of the *Actinomyces coelicolor* species-group. Journ. Bact., 44:555–570.

STANIER, R. Y., and C. B. VAN NIEL

1941. The main outlines of bacterial classification. Journ. Bact., 42. 437–466.

STILLE, B.

1937. Zytologische Untersuchungen an Bakterien mit Hilfe der Feulgenschen Nuclealreaktion. Arch. Mikrobiol., 8:125–148.

TATUM, E. L., and J. LEDERBERG

1947. Gene recombination in the bacterium, *Escherichia coli*. Journ. Bact., 53:673–684.

TULASNE, R.

1947. Sur la mise en évidence du noyau des cellules bactériennes. Compt. Rend. Soc. Biol., 141:411–413.

1949a. Sur la cytologie des bactéries vivantes étudiées grâce au microscope à contraste de phase. Compt. Rend. Soc. Biol., 143:1390–1392.

1949b. Données nouvelles sur la cytologie des bactéries apportées par la microscopie de contraste. Compt. Rend. Soc. Biol., 143:1392–1394.

TULASNE, R., and R. MINCK

1947. Mise en évidence des noyaux des cocci par la ribonucléase. Compt. Rend Soc. Biol., 141:1255–1256.

TULASNE, R., and R. VENDRELY

1947. Mise en évidence des noyaux bactériens par la ribonucléase. Compt. Rend. Soc. Biol., 141:674–676.

WELSCH, M., and E. NIHOUL

1948. A propos de la mise en évidence du noyau bactérien. Compt. Rend. Soc. Biol., 142:1449–1452.

WINOGRADSKY, S.

1949. Microbiologie du Sol. Oeuvres complètes. 861 pp. Paris: Masson et Cie.

1952. Sur la classification des bactéries. Ann. Inst. Pasteur, 82:125–131.

WINSLOW, C. E.-A.

1914. The characterization and classification of bacterial types. Science, 39:77–91.

WINSLOW, C. E.-A., *et al.*

1917. Suggested outline of bacterial classification. Journ. Bact., 2:505–566.

1920. The families and genera of the bacteria. Journ. Bact. 5:191–229.

CLASSIFICATION OF THE ALGAE[1]

By GEORGE F. PAPENFUSS
University of California, Berkeley

Introduction

A general treatment of such a heterogeneous assemblage of organisms as the algae may fittingly be introduced with a statement of the criteria used in the delimitation of the group.

These plants are readily separated from those next above them in the evolutionary scale, the archegoniate plants, by the fact that their reproductive organs lack a primarily produced sterile jacket of cells. (The antheridium of the Charophycophyta is an exception.) The separation of some algae from certain members of the other groups of simple organisms, such as the bacteria, the fungi, and the protozoa, is much more difficult and not infrequently the assigning of an organism to the algae or to one of these groups is a purely arbitrary procedure.

Although the major taxa of algae show little or no relationship to one another, the group as a whole is clearly distinguished from other simple organisms by the ability of a great majority of the species to synthesize organic compounds by the process of photosynthesis. There are many exceptions to this rule but the saprophytic, parasitic, or holozoic forms usually reveal their alliance to autotrophic types by their structure, life history, and storage products. In very many instances the heterotrophic forms appear to have been derived from photosynthetic types. The autotrophic bluegreen algae may be distinguished from the autotrophic bacteria by their possession of chlorophyll *a* and the evolution of oxygen as a by-product of photosynthesis.

In modern systems of classification the algae comprise more than half the number of plant phyla. Of the known species, however, they constitute less than 10 per cent. The disproportionately large number of major algal taxa reflects the great diversity in the structure, reproduction, and metabolism of these plants as contrasted with the remainder of the plant kingdom.

Within the confines of this brief treatment, my review of the history of the classification of the group of necessity will be confined to the broad outlines of the system. Attention will also be given to the history of the discovery of sex in the algae and to the growth in knowledge of their life histories since advances in these aspects of phycology have almost always contributed to a better understanding of the interrelationships and phylogeny of the groups concerned.

The nomenclature of the majority of algae, like that of most plant groups,

---

1. I am deeply indebted to Dr. Johannes Proskauer for critically reading the manuscript and for his many constructive suggestions. I should also like to thank Professor G. M. Smith and Dr. T. V. Desikachary for kindly reading the manuscript and making helpful suggestions.

begins with Linnaeus' (1753) *Species plantarum.* It is of interest to note that in Linnaeus' system the algae were grouped along with the pteridophytes, mosses, and fungi in a single class, the Cryptogamia, whereas the phanerogams were divided into 23 classes. Linnaeus recognized 14 genera of algae but only four of them (*Conferva, Ulva, Fucus,* and *Chara*) comprised algae in the current sense and two others (*Byssus* and *Tremella*) included a few species of algae. During the following fifty years botanists were content to accept the classification of Linnaeus and, with very few exceptions, always referred their algal species to his genera. Usually, *Conferva* received the filamentous, *Ulva* the membranous, and *Fucus* the fleshy forms, and treatises were written on the largest of these three genera, namely, *Fucus* and *Conferva* (e.g., by Gmelin, 1768; Esper, 1797–1808; Dillwyn, 1802–1809; Vaucher, 1803; Lamouroux, 1805; Turner, 1808–1819). *Chara* was frequently excluded from the algae.

Stackhouse was the first to break away completely from the custom of recognizing only the Linnean genera of algae. He concerned himself especially with the British species of the marine genus *Fucus,* and his study of them brought him to the realization that this comprehensive genus comprised a large number of distinct taxa which he accordingly removed to new genera. In a series of three works (1795–1801, 1809, 1816) he divided *Fucus* into 67 genera (including one, *Pygmaea,* now known to be a lichen). Papenfuss (1950a) has typified Stackhouse's genera and has discussed their fate.

In 1813 Lamouroux published his *Essai sur les genres de la famille des thallasssiophytes non articulées,* which formed an important advance in that he, in addition to establishing a number of new genera, mostly as segregates from *Fucus,* proposed a system of classification of the algae into major taxa (orders) based in part on color.

C. Agardh (1817, 1824) and especially Harvey (1836) made significant modifications in Lamouroux' system. Harvey divided the algae with which he was concerned into the four divisions (phyla) Melanospermeae (brown algae), Rhodospermeae (red algae), Chlorospermeae (green algae), and Diatomaceae (diatoms and desmids). Without realizing it, Lamouroux and Harvey thus introduced a biochemical character into the classification of the algae. Subsequent investigations have firmly established the soundness of this character as an indicator of phylogenetic affinity. On the basis of pigment composition and other characters of seemingly comparable merit several major taxa, in addition to Harvey's original four, have now been recognized. In the present treatment the assemblage is considered as comprised of seven phyla and in addition three classes, one of which, the Schizophyceae (bluegreen algae), is regarded as constituting along with the class Schizomyceteae (bacteria) the phylum Schizophyta, and two of which are composed of forms of uncertain affinity. The history of these major groups is reviewed in the separate sections into which the body of this chapter is divided.

In 1836, Endlicher divided plants into two kingdoms—Thallophyta and Cormophyta. The designation Thallophyta was later used as a phyletic name for all plants below the level of the Bryophyta. Although the term still has merit as denoting plants of a certain morphological type, it is now generally recognized that the various classes of algae and fungi can no longer be regarded as belonging to a single phylum.

For a long time all algae exhibiting movement—diatoms, desmids as well as flagellated green, yellow-green and golden-brown forms—were automatically regarded as animals. Although the zoologists in the course of time relinquished the diatoms and desmids, the flagellated forms and their amoeboid relatives (but frequently not their nonmotile unicellular and multicellular relatives) are still considered as belonging to the artificial phylum Protozoa.

Among the early biologists who regarded some of the flagellated organisms as algae rather than protozoa are Siebold (1848, 1849), Braun (1851), and Cohn (1852). The bulk of the so-called Flagellata, however, for a long time remained the exclusive domain of zoologists. Klebs (1883) was the first to emphasize the plantlike nature of many of these forms and in the ensuing years the group Flagellata received increasing attention from botanists and was included among the algae in treatises on the plant kingdom (Warming, 1890; Engler, 1898; Senn, 1900; and others). Epoch-making contributions that revealed the intimate relationship of some of these forms to nonflagellated unicellular and multicellular or so-called "algal" types were made by Bohlin (1897a, 1897b), Luther (1899), Klebs (1912), and Pascher (1912b, 1914). The history of this change in the outlook of botanists in regard to the systematic position of the flagellates is reviewed in the appropriate sections below, especially in that on the Euglenophycophyta.

The discoveries and growth in knowledge of sex in plants form an extremely interesting chapter in the history of botany. The algae provide particularly favorable material for the study of sex and have been used to advantage in this connection since the middle of the last century (cf. Kniep, 1928).

Although numerous observations had been made on the reproduction of algae before 1853 and many botanists had come to believe that some algae exhibited a sexual process, the established facts in support of such a view were extremely meager. Some forms appeared in places and under circumstances that necessitated the assumption of spontaneous generation. In this way, Meyen (1827) explained the appearance of small algae, known as "Priestley's matter," in stagnant water and even in closed vessels. Kützing (1833a) and others put forth the view that the simplest algae once produced spontaneously could develop according to circumstances into a variety of algae. When the zoöspores of an undisputed alga were seen in the process of liberation from the thallus, the phenomenon was interpreted as a changing of the plant into an animal. The remarkable thing is not so much that such views were entertained but that the majority of biologists of the time combined with them a belief in the immutability of species.

The first alga suspected of showing a sexual process was *Spirogyra*. Hedwig (1798) was of the opinion that the zygospores, which were discovered by O. F. Müller in 1782, were formed as the result of a sexual act. Vaucher (1803) also studied conjugation in *Spirogyra* and related forms but he, like many later botanists, was not fully convinced of the sexual nature of this process since it was difficult to conceive of a sexual process without the criterion of a morphological difference between the sex organs; and furthermore, it was evident that one and the same filament could both deliver and receive substance from a neighboring filament. During the first half of the nineteenth century and for some time afterward (as recently as 1916 and 1926 by West [1916, p. 135] and Schiffner [1926]) a sharp distinction was made between fertilization (the union of morphologically different cells) and conjugation (the union of cells of like form). Thwaites (1848), the discoverer of conjugation in diatoms, was the first to regard conjugation as a sexual process without qualification.

Vaucher (1803) also studied the genus that was later named for him (*Vaucheria*) and designated as sex organs the structures now referred to as antheridia and oögonia. Vaucher was far in advance of his time, however, and his conclusions were not accepted. As late as 1847 Nägeli, for instance, thought that red algae were the only algae that reproduced sexually but even in this assumption he was entirely wrong inasmuch as he believed the tetrasporangia to be the female sex organs.

The turning point in the outlook of botanists occurred with the appearance of Thuret's papers of 1853 (a and b) and 1854. He established that in *Fucus* only eggs to which sperms had had access would germinate. Shortly afterward, Pringsheim (1855, 1856) observed the penetration of the sperm into the egg of *Vaucheria* and *Oedogonium*. At first the exact function of the sperm in sexual reproduction was not understood, but it seemed doubtful that it actually fused with the egg. Pringsheim's observations were quickly confirmed, however, by a number of workers. Cohn (1855, 1856) established the occurrence of sexuality in *Sphaeroplea* and *Volvox*, De Bary (1858a) confirmed the findings of Pringsheim in regard to *Vaucheria* and *Oedogonium*, and Pringsheim (1860) published his observation on *Coleochaete*.

The majority of forms studied during this early period showed oögamous sexual reproduction. The first report of a conjugation of motile isogametes was by Pringsheim in 1870 in regard to *Pandorina*. This genus thus bridged the gap between the oögamous types and the condition as shown by *Spirogyra* and diatoms. Shortly afterward isogamous sexual reproduction was discovered in a number of other algae and sufficient evidence was brought to bear to dispel the old belief that conjugation and fertilization were different processes.

Hertwig in 1876, working on a species of sea urchin, showed for the first time that a significant feature of sexual reproduction was the fusion of the gamete nuclei. Schmitz (1879c) observed a similar fusion of nuclei for the first time in plants in *Spirogyra* and Berthold (1881) next saw it in the brown alga *Ectocarpus*. In the words of Möbius (1937, p. 345):

> Die Kryptogamen waren somit mehr phanerogam geworden als die Phanerogamen, für die man zwar die Differenzierung der Geschlechter und die Notwendigkeit der Bestäubung erkannt hatte, die aber in Hinsicht auf den eigentlichen Vorgang der Befruchtung noch ganz kryptogam geblieben waren.

Phylum Chlorophycophyta

Characterization: This phylum is comprised of a large and diversified assemblage of algae, ranging from motile and nonmotile unicellular forms to massive coenocytic types, such as certain species of *Codium*. The majority of species are aquatic. Some genera (e. g., *Pleurococcus*, *Trentepohlia*, *Fritschiella*) are terrestrial or subaerial in occurrence. Certain orders (Siphonocladales, Dasycladales) are wholly marine, others (Zygnematales, Oedogoniales) are freshwater in distribution. Several orders and even some genera (e. g., *Chlamydomonas*, *Cladophora*) have both marine and freshwater representatives.

In the majority of species the cell is provided with a definite wall which is usually composed of an inner, and often stratified, cellulosic layer and an outer pectic layer. In the Siphonales the cellulose is frequently replaced by callose. In the Dasycladales and in many Siphonales the pectic layer of the wall is impregnated with calcium carbonate. (In some seas the lime-incrusted fronds of *Halimeda* form an important constituent of coral reefs.) In the desmids and a few other forms the wall consists of two overlapping pieces.

The chloroplasts are usually well defined and ordinarily lie in the peripheral cytoplasm, but axile plastids are not uncommon and are especially characteristic of the desmids. According to the genus or species, the cells are provided with one or more plastids of varying form and size. The pigment complex is essentially the same as in higher plants, consisting of chlorophyll *a*, chlorophyll *b*, xanthophylls, and carotenes. The Siphonales contain two xanthophylls (siphonein and siphonaxanthin) that are peculiar to them (Strain, 1951). A few forms (e. g., *Polytomella*) are colorless. The customary food reserve is starch. In many species the chloroplasts contain pyrenoids. Usually, the pyrenoid is enclosed by a starch envelope consisting of separate plates of starch.

In the majority of green algae the vegetative cells are uninucleate. The Sphaeropleales, Cladophorales, Siphonocladales, and many Chlorococcales have multinucleate cells, and the nonseptate filaments of the order Siphonales are, of course, also multinucleate.

Except in the Polyblepharidaceae of the order Volvocales, the Oedogoniales, and *Derbesia* (Siphonales) the motile stages are provided with two or four terminal flagella that are of equal length and devoid of cilia. In the Polyblepharidaceae the cells bear two, three, four, five, or more flagella of equal length and in the Oedogoniales and in *Derbesia* the reproductive cells bear a subterminal collar of many equal flagella.

Asexual reproduction by ordinary cell division is of common occurrence in the unicellular forms. Many species reproduce by zoöspores. In most instances the cells in which the zoöspores are produced are not differentiated as specialized sporangia. The zoöspores are formed singly or in numbers by the cell contents. Nonmotile spores (aplanospores, akinetes) are produced in a number of genera.

Sexual reproduction has been established for a large number of genera representative of all the orders, with the possible exception of the Schizogoniales (cf., however, Fujiyama, 1949). The species may be monoecious or dioecious and isogamous, anisogamous, or oögamous. In isogamous and anisogamous forms the gametangia may or may not be morphologically differentiated structures. Oögamous forms ordinarily produce differentiated oögonia and antheridia—*Sphaeroplea* is an exception to the rule. Except in *Sphaeroplea*, only one egg is formed in each oögonium. The egg is ordinarily fertilized in position within the oögonium. In a few instances (*Chlorangium oögamum, Chaetonema irregulare*) it is extruded prior to fertilization. There is clear evidence that oögamy has evolved independently in several of the orders.

In almost all freshwater species, the zygote is a thick-walled resting cell. In marine species, on the contrary, it is a thin-walled cell which ordinarily germinates directly. It thus seems reasonable to assume that those freshwater species in which the zygote is not a resting cell are derived from marine species or conversely that the marine species in which the zygote is a resting cell are derived from freshwater species.

A large majority of the green algae and almost all the freshwater representatives of the phylum apparently are haploid, with meiosis occurring in the germinating zygote. Certain representatives of the orders Volvocales, Ulotrichales, Cladophorales, and possibly some Chlorococcales and Siphonales, show an alternation of generations. The Siphonocladales, the majority of the Siphonales and the Dasycladales are diploid as far as known, with meiosis occurring at gametogenesis. The Volvocales constitute a basic group from which the other orders apparently have evolved.

History: Recognition of the Chlorophycophyta as an autonomous group begins with Lamouroux (1813) who, largely on the basis of color, established an "ordre" Ulvacées to receive certain genera of green algae, *Ulva, Bryopsis, Caulerpa,* and *Asperococcus. Asperococcus,* however, was later shown to belong to the brown algae. Harvey (1836) erected the "division" Chlorospermeae and assigned to it not only the green algae but also the bluegreen algae and a few genera that were later found to be red or brown algae. The currently accepted class name Chlorophyceae was proposed by Kützing (1845).

By the middle of the last century, a comparatively large number of genera of unicellular green algae—both flagellated and nonflagellated forms—had been described, mostly by Ehrenberg (1838 and earlier), Nägeli (1849), and others. Many of these genera, however, were regarded as animals, the gutless stomach animalcules of Ehrenberg.

In 1819, Lyngbye described the genus *Palmella* and in 1824 C. Agardh described *Protococcus.* Since these two genera of unicellular algae were comprised of nonmotile forms (cf., however, Silva and Starr, 1953, regarding *Protococcus*) they were accepted as algae rather than animals from the beginning. Recognizing the distinctiveness of *Palmella* and *Protococcus* as contrasted with the genera that constituted the Ulvaceae (which received mostly membranous forms) and the Confervaceae (which received mostly filamentous forms), Endlicher (1843) created for them and various other unicellular genera the suborder Palmellae, which he placed in the "order" Confervaceae. The Palmellae were in turn subdivided by Endlicher into the two tribes Protococcoideae (which received *Protococcus*) and Coccochloreae (which included *Palmella*).

Kützing (1833b) was the first to recognize the differences between the diatoms and the desmids, for the latter of which he established the family Desmidiaceae. He (1843, 1845, 1849) placed this family in a separate group Chamaephyceae (dwarf algae), which he (1845) assigned to the Chlorophyceae. The Chamaephyceae also received, among others, the Palmellae, which Kützing regarded as a family. Hassall (1845) erected a separate family Protococceae for *Protococcus* and several other genera.

Since these early beginnings, the Palmellaceae and Protococcaceae have had an extensive and involved taxonomic history. For a long time they functioned as a catch-all for many different kinds of unicellular and colonial algae.

Siebold (1849), Nägeli (1849), Braun (1851), and Cohn (1852, 1854) regarded as algae certain unicellular and colonial motile green organisms such as *Chlamydomonas, Gonium* (first recognized as an alga by Turpin, 1828a, pp. 322–329), *Pandorina, Stephanosphaera,* and *Volvox* (all members of the Volvocales). Cohn at first (1852) placed these organisms in the "order" Palmellaceae but in 1856 considered them as constituting the family Volvocaceae. Rabenhorst (1863, 1868) grouped the Volvocaceae along with the Palmellaceae and Protococcaceae in a common order which he (1868) called Coccophyceae.

The relationship between the Zygnemataceae and the Desmidiaceae was recognized by Nägeli (1849) and others but it was De Bary (1858b) who first furnished conclusive proof of this. He united these two groups in a "family" Conjugatae.

In his important work on the freshwater algae of Europe, Rabenhorst (1868) divided the green algae in accordance with the system of Stizenberger (1860) into four orders: (1) Coccophyceae, with the families Palmellaceae, Protococcaceae, and Volvocaceae; (2) Zygophyceae, with the families Desmidieae and Zygnemeae; (3) Siphophyceae, with the families Hydrogastreae (= Botrydiaceae) and Vaucheriaceae; and (4) Nematophyceae, with the families Ulvaceae, Sphaeropleaceae, Confervaceae, Oedogoniaceae, Ulotrichaceae, Chroolepidiaceae (= Trentepohliaceae), and Chaetophoraceae. The separation of the Chlorophycophyta into the four orders recognized by Stizenberger (but later, for example, by De Toni [1889] and Wille [1890–1891], usually called Protococcoideae, Conjugatae, Siphoneae, and Confervoideae, respectively) remained in force until the beginning of the present century.

The classification of the unicellular and colonial green algae (other than the desmids, whose relationship with the Zygnemataceae is clear) and of the siphonous forms has always been fraught with many difficulties. It is the sorting out of these algae that will be considered especially in the following pages.

In agreement with Rabenhorst, Kirchner (1878) grouped the families Volvocaceae, Protococcaceae, and Palmellaceae in a common order which he named Protococcoideae. Hansgirg's (1888a) and Wille's (1890–1891) circumscriptions of the order Protococcoideae were much the same as that of Kirchner, except that Hansgirg merged the Protococcaceae in the Palmellaceae whereas Wille recognized a larger number of families.

The far-reaching contributions by Klebs (1883, 1892) and Luther (1899), which resulted in the removal of the euglenids from the Protococcoideae and the establishment of a separate class Heterokontae for those "green" algae with two unequal flagella, are considered under the Euglenophycophyta and Chrysophycophyta, respectively.

Blackman (1900) and Blackman and Tansley (1902) arrived at the significant conclusion that the order Protococcoideae comprised families representative of three divergent vegetative tendencies which furnished the phylogenetic lines on which the different types could be arranged. (1) Those forms in which the plant body is motile by means of flagella during the vegetative phase. (2) Those in which the plant body is not motile and in which the cells are uninucleate and divide during the vegetative phase. (3) Those in which the plant body is nonmotile and in which the cells do not undergo vegetative division but the nucleus divides and the cells consequently become multinucleate.

As delimited in the arrangement at the end of this section, these three lines are represented by various orders and families as follows. The first group corresponds to the Volvocales. The second group is represented by the suborder Tetrasporineae of the order Volvocales and the family Pleurococcaceae of the Ulotrichales. The third group is represented by the order Chlorococcales. (In the breaking up of the heterogeneous order Protococcoideae [= Protococcales Kirchner orth. mut. Engler, 1892], the ill-fated designation Protococcales has fortunately been relegated to synonymy. Silva and Starr, 1953, have produced convincing evidence that the type species of *Protococcus* C. Agardh is actually a species of *Haematococcus* rather than of the plant that is commonly known as *Protococcus* but which probably should be known as *Pleurococcus*. Furthermore, it is now known that the unicellular habit of this genus is a derived rather than a primary condition and that it belongs in the Ulotrichales.)

The classification of the multinucleate segmented (exclusive of the Hydrodictyaceae) and the siphonous Chlorophycophyta has also been a matter of much confusion and disagreement. Egerod (1952) has recently given an excellent treatment of the taxonomic history of these algae; a brief review will consequently suffice here.

Greville (1830) established the "order" (family in the modern sense) Siphoneae to accommodate certain green algae (*Codium, Bryopsis, Vaucheria, Botrydium*) that possess a tubular, nonseptate thallus. (He placed *Caulerpa* in its own "order.") In the course of time a number of additional families were erected, especially by Kützing (1843, 1849), to receive various genera belonging to the siphonous complex, among which are the Sphaeropleaceae, Cladophoraceae, Valoniaceae, Caulerpaceae, and Dasycladaceae (a group comprised of calcified plants that for a long time were thought to be corals). Stizenberger (1860) arranged the algae belonging to this complex in his order Siphophyceae (except for the Sphaeropleaceae and Cladophoraceae, which he placed in the Confervaceae of his order Nematophyceae). This order was comprised of the families Valoniaceae (in which he included *Caulerpa*), Vaucheriaceae (now placed in the Xanthophyceae of the Chrysophycophyta), Codiaceae, and Dasycladaceae.

Schmitz (1879a) created the group Siphonocladaceae to receive his new genus *Siphonocladus* and a number of other multinucleate septate or saccate genera (e.g., *Valonia, Microdictyon, Cladophora,* and *Botrydium,* which genus is now known to belong to the Xanthophyceae).

Starting with Bohlin's paper of 1901, the complex of siphonous algae has been segregated into six orders. Bohlin erected the order Vaucheriales and removed it to the class Heterokontae. Blackman and Tansley (1902) substituted the ordinal name Siphonales for the designation Siphophyceae or Siphoneae and divided the order into the two suborders Siphoneae (which received nonseptate genera) and the Siphonocladeae (which received septate forms such as *Siphonocladus, Cladophora, Valonia, Sphaeroplea,* and many other genera). Oltmanns (1904) elevated the suborder Siphonocladeae to the rank of order (Siphonocladales) and placed in it the five families Siphonocladaceae, Cladophoraceae, Sphaeropleaceae, Valoniaceae, and Dasycladaceae.

West (1904) removed the Cladophoraceae and Sphaeropleaceae to an autonomous order Cladophorales. As characterized by him this order conformed closely to Oltmanns' Siphonocladales and in 1916 West merged the Cladophorales in the Siphonocladales. Heering (1921) and Oltmanns (1922a) not only followed West but in conformity with Oltmanns' classification of 1904 extended the concept of the Siphonocladales to include even the nonseptate Dasycladaceae. In the intervening period, however, Børgesen (1905, 1913) had discovered in *Siphonocladus* and related genera the peculiar method of cell division termed segregative division by him. Despite the distinctiveness of this character disagreement has persisted with respect to the autonomy of one or the other of these two orders. Some authors (e.g., Fritsch, 1935, 1947) have accepted the Cladophorales but place the genera comprising the Siphonocladales in the Siphonales, whereas others (e.g., Feldmann, 1938) have recognized the Siphonocladales as a distinct order but have included in it the genera constituting the Cladophorales. Egerod (1952) has given a careful analysis of this confusing state of affairs and has detailed the evidence favoring recognition of all three orders.

As has been pointed out by Fritsch (1944) and Egerod (1952) the Anadyomenaceae (at least as far as *Anadyomene* and *Microdictyon* are concerned) depart from other Siphonocladales in not exhibiting segregative division. Both these authors have also brought attention to the correspondence between this family and the Cladophoraceae. The Anadyomenaceae are here transferred from the Siphonocladales to the Cladophorales.

In 1931 Pascher removed the Dasycladaceae from the Siphonocladaceae and erected for them the order Dasycladales, a group distinguished by the formation of operculate cysts and certain other features. It is now known (Hämmerling, 1931) that the members of this order are actually uninucleate during their vegetative phase and become multinucleate only when they become fertile.

The status of the monogeneric family Sphaeropleaceae remains to be considered. Owing to the multinucleate condition of the septate thallus, *Sphaeroplea* was for a long time associated either with the Siphonocladales or the Cladophorales. As has been emphasized by Fritsch (1929; 1935, pp. 224–225; 1947, pp. 43–48), however, *Sphaeroplea* possesses a number of characters that appear to ally it with the Ulotrichales rather than the complex of siphonous orders considered above, which Egerod (1952) would derive from the Chlorococcales. Fritsch (1935) considers *Sphaeroplea* as constituting a suborder in the Ulotrichales. Prescott (1951) has elevated this suborder to the rank of order. I concur with the view of Prescott.

In addition to the orders which have so far been considered, namely, the Volvocales (including the Tetrasporales), Chlorococcales, Cladophorales, Siphonocladales, Siphonales, Dasycladales, and Sphaeropleales, the Chlorophycophyta have been credited in recent times with the following orders: Zygnematales (= the order Zygophyceae of Stizenberger), Ulotrichales, Chaetophorales, Ulvales, Microsporales, Cylindrocapsales, Oedongoniales, and Schizogoniales. These orders, with the exception of the Zygnematales, constitute the bulk of the Nematophyceae of Stizenberger.

The Zygnematales (Conjugales of some authors) embrace a well-marked group of algae characterized by the conjugation of nonflagellated gametes. The relationship of the essentially unicellular desmids with the filamentous Zygnemataceae (which family includes the classical *Spirogyra*) has been generally recognized since the time that De Bary (1858) pointed to their alliance. The Zygnematales occupy an isolated position in the Chlorophycophyta. At one time the order was regarded by some authors (e.g., Engler and Gilg, 1924) as sufficiently distinct from the other green algae to merit recognition as an independent phylum. There seems to be little justification, however, for considering the Zygnematales as distinct from the Chlorophycophyta, and in recent systems of classification the assemblage has usually been treated as an order of the Chlorophycophyta. It is not inconceivable that the Zygnematales evolved, in the distant past, from the Volvocales. Monographic treatments of the order or of some of its families have in recent times been published by Czurda (1932, 1937), Krieger (1933–1937, 1939), Kolkwitz and Krieger (1941–1944), and Transeau (1951). The classification of the Zygnematales adopted in the arrangement at the end of this section is essentially that of Fritsch (*in* West, 1927).

The Ulotrichales as here accepted include the Chaetophorales, Ulvales, Microsporales, and Cylindrocapsales. The order Chaetophorales was established by Wille (1901) to receive essentially the same algae, including *Ulothrix,* that Borzi (1895) assigned to his order Ulotrichales. In current systems of classification the Chaetophorales are either accepted as an autonomous order (e.g., by Fritsch, 1935) or they are merged in the Ulotrichales (e.g., by Smith, 1950). Fritsch (1935; 1939; 1944, p. 245) especially, has argued for the retention of the order, primarily because of the heterotrichous habit of the majority of the forms. However, in some genera of the Chaetophorales either the prostrate or the erect system may be absent or poorly developed (cf. Papenfuss, 1951b). Heterotrichy has evolved independently in a number of different groups of algae—simple forms as well as advanced types—and it is doubtful that any great weight should be placed on this character in the delimitation of major taxa. In the family Acrochaetiaceae of the red algae, for instance, some species of a genus have a single basal cell whereas others produce an extensive prostrate system.

Although the majority of recent systematists have accepted the order Ulvales, proposed by Blackman and Tansley (1902), there is a great deal of justification for the view of Fritsch (1935, 1944) that they are advanced Ulotrichales. The possession by the Ulvales of a parenchymatous thallus does not distinguish them from all Ulotrichales since some of the latter (e.g., *Fritschiella*) also form parenchymatous thalli. Some Ulvales show an alternation of isomorphic generations but this is now believed to be true also of certain Ulotrichales (e.g., *Draparnaldiopsis* and *Fritschiella;* Singh, 1945, 1947).

The order Microsporales, which was established by Bohlin (1901) to accommodate the genus *Microspora,* has never received wide acceptance. Recently, however, it was resurrected by Prescott (1951), who in the same work also erected an order Cylindrocapsales for the genus *Cylindrocapsa.* Although these two genera, especially the oögamous *Cylindrocapsa,* occupy a somewhat isolated position among the Ulotrichales it seems best to regard them in agreement with Fritsch (1935) and Smith (1950) as constituting well-defined families within the Ulotrichales. Printz (1927) does not even recognize the family Microsporaceae; he places *Microspora* in the Ulotrichaceae.

The Oedogoniales occupy an isolated position in the Chlorophycophyta. The peculiar method of cell division shown by the three genera comprising the order is not met with anywhere else and the collar of subterminal flagella present in the sperms and zoöspores is encountered elsewhere only in *Derbesia* (Siphonales). Monographic treatments of the order have been presented by Hirn (1900), Tiffany (1930), and Gemeinhardt (1938–1940).

The Schizogoniales, established by West (1904), comprise a small group of terrestrial, freshwater, and marine algae placed by some (e.g., Fritsch, 1935) in one, by others (e.g., Knebel, 1935) in two, genera. The group is characterized by the formation of parenchymatous thalli, stellate plastids, and the apparent lack of motile reproductive cells (cf., however, Fujiyama, 1949). The order has recently been the subject of a monograph by Knebel (1935).

The more important early discoveries relating to sexuality in the green algae have been considered briefly in the introduction to this chapter. In the present section attention will be focused especially on some of the more recent work on the life histories and the associated nuclear phenomena.

A fusion of the gamete nuclei in the zygote was observed by Schmitz (1879c) in *Spirogyra.* Klebahn (1888, 1891, 1892) observed it in desmids and *Oedogonium,* and Goroschankin (1890) saw it in *Chlamydomonas.*

Following the postulate of Weismann (1887) that the doubling of the chromatin mass at syngamy must be followed by a regulatory reducing process, many investigations were undertaken with the view of testing this hypothesis and of determining the place in the life history where the reduction may occur. The first observations on meiosis in the green algae were by Allen (1905) in *Coleochaete.* The life history of *Coleochaete* had previously been investigated by Pringsheim (1860) who showed that the contents of the zygospore at germination divide into a number of cells, each of which later gives rise to a zoöspore. Pringsheim and others regarded this structure as the sporophyte of *Coleochaete.* Allen established, however, that meiosis occurs during the first two divisions of the germinating zygote and that the cellular structure produced by the zygote is haploid. Thus Allen eliminated the only green alga that till then was regarded as exhibiting an alternation of generations. Cytological studies by various later workers on diverse green algae confirmed the observations of Allen and until 1925 it was generally held that green algae are haploid, with meiosis always occurring during the germination of the zygote.

Since 1925 when Miss Williams showed that *Codium* is a diploid alga, our concept of the life histories of the green algae and the associated nuclear cycles has undergone a profound change. It is now known that the Siphonocladales (Schechner-Fries, 1934; Schussnig, 1938), Siphonales (Williams, 1925; Schussnig, 1930, 1932, 1939, 1950; Zinnecker, 1935), and Dasycladales (Schulze, 1939) are diploid algae, at least those that have been studied cytologically, and that it is the diploid soma that in them, as in the Fucales, diatoms, and animals, functions as the gamete producing generation. (See, however, the statements below on *Derbesia* and *Halicystis.*)

The occurrence of an alternation of isomorphic generations in the green algae was first demonstrated by Hartmann (1929) and Føyn (1929, 1934a, 1934b) in members of the orders Cladophorales (*Cladophora, Chaetomorpha*) and Ulotrichales (*Enteromorpha, Ulva*). Singh (1945, 1947) has reported the occurrence of a similar cycle in *Draparnaldiopsis* and *Fritschiella* (both Ulotrichales), and Iyengar and Ramanathan (1940, 1941) have established its occurrence in *Anadyomene* and *Microdictyon* (both here placed in the Cladophorales).

Juller (1937) has shown that *Stigeoclonium subspinosum* (Ulotrichales) possesses an alternation of heteromorphic generations, with the diploid asexual generation smaller than the haploid one. Jorde (1933) has brought forth fairly convincing evidence indicating that certain species of the unicellular *Codiolum,* a genus of the family Chlorococcaceae in the order Chlorococcales, represent the diploid asexual generation of species of the filamentous *Urospora,* a member of the family Cladophoraceae in the Cladophorales. These observations still require corroboration, but if they should prove to be correct, we would have here an alternation of heteromorphic generations, representing two kinds of green algae which for a long time have been regarded as phylogenetically very far apart.

Kornmann (1938) and Feldmann (1950) have made observations suggesting that *Halicystis* and *Derbesia* also constitute phases in the life history of one and the same alga, with *Halicystis* representing the gametophytic and *Derbesia* the sporophytic generation. These two genera have been regarded as the type representatives of two distinct families, Halicystidaceae and Derbesiaceae, of the order Siphonales. In view of the fact that *Derbesia* is the only genus of green algae outside the order Oedogoniales that is known to possess swarmers with a subterminal collar of flagella and that *Halicystis* forms terminally biflagellate gametes, the apparent existence of an intimate relationship between these two kinds of plants is a matter of far-reaching significance.

Although the majority of Chlorococcales appear to be haploid, there is some indication that *Chlorochytrium Lemnae* shows an alternation of generations

(Kurssanov and Schemakhanova, 1927) and that *Apiococcus consociatus* is diploid (Korshikov, 1926).

Among the more remarkable discoveries of recent times are those showing that even the Volvocales include forms exhibiting an alternation of generations. Thus it has been shown by Strehlow (1929) and Behlau (1935) that *Chlorobrachis gracillima* is the diploid motile stage of *Pyrobotrys gracilis.* Two other species of *Pyrobotrys* likewise have a motile zygote (Behlau, 1935). Behlau (1939) has also shown that *Carteria ovata* is the diploid motile stage of *Chlamydomonas variabilis.*

Judged by their morphology, especially that of the motile cell, the Chlorophycophyta show affinities only with the Charophycophyta. The possession by the Euglenophycophyta of chlorophyll *a* and chlorophyll *b* suggests that this phylum is related to other green plants. Morphologically the euglenid cell is very different, however, from the motile cell of the green algae, and whatever relationship there may be between these two groups probably is extremely remote. Fossil Chlorophycophyta are known from the Ordovician onward.

The following synoptic outline of the Chlorophycophyta is adapted largely from Fritsch (1935), Smith (1950), and Egerod (1952).

Phylum CHLOROPHYCOPHYTA Papenfuss (1946, p. 218)
  Syn.: Chlorophyta Pascher (1914, p. 158); Glaucophyta Skuja (1948, p. 63)
    Class CHLOROPHYCEAE Kützing (1843, p. 118)
      Syn.: Chlorospermeae Harvey (1836, p. 163); Glaucophyceae Bohlin (1901, p. 16); Chlorophyllaceae Rabenhorst (1863, p. 117); Chlorophyllophyceae Rabenhorst (1868, p. 1); Zygophyceae Rabenhorst (1868, pp. 1, 101); Isokontae Blackman et Tansley (1902, p. 20); Akontae Blackman et Tansley (1902, p. 168); Stephanokontae Blackman et Tansley (1902, p. 166); Prasinophycinées Chadefaud (1950b, p. 988); Euchlorophycinées Chadefaud (1950b, p. 988); Pocillophycinées Chadefaud (1950a, p. 788)
        Order VOLVOCALES Oltmanns (1904, p. 133)
          Syn.: Chlamydomonadales Fritsch, *in* West (1927, p. 67); Chlorodendrales Fritsch, *in* West (1927, p. 67); Pyramidomonadales Chadefaud (1950b, p. 988); Tetrasporales Lemmermann (1915, p. 21)
            Suborder **Volvocineae** West (1916, p. 161)
              Syn.: Chlamydomonadineae Fritsch (1935, p. 78)
                Family Polyblepharidaceae (Blackman et Tansley) Oltmanns (1904, p. 135)
                  Syn.: Polytomellaceae (Blackman et Tansley) Skuja (1930, p. 158)
                Family Pedinomonadaceae Korschikov (1938; not seen, cited from Skuja, 1939b)
                Family Nephroselmidaceae Pascher (1913b, p. 110)
                  (See Skuja, 1948, pp. 65, 66, 367)
                Family Chlorovittaceae Schiller (1925b, p. 104)
                Family Chlamydomonadaceae Stein orth. mut. G. M. Smith (1920, p. 90)
                  Syn.: Carteriaceae G. M. Smith (1920, p. 92); Sphaerellaceae (Schmidle) West (1916, p. 166)
                Family Haematococcaceae (Trevisan) Marchand orth. mut. G. M. Smith (1950, p. 109)
                  Syn.: Protococcaceae (Endlicher) Hassell orth. mut. Nägeli (1847, p. 153; as to type only cf. Silva and Starr, 1953)
                Family Spondylomoraceae (Ehrenberg) Korschikov (1923, p. 178)
                Family Astrephomenaceae Pocock (1954, p. 126)
                Family Volvocaceae Ehrenberg orth. mut. Cohn (1856, p. 323, as Volvocinées)
                  Syn.: Pandorinaceae Luerssen orth. mut. Eichler (1880, p. 4)

Family Phacotaceae (Bütschli) Oltmanns (1904, p. 147)
Suborder **Tetrasporineae** West (1916, p. 182)
Family Palmellaceae (Endlicher) Kützing orth. mut. Nägeli (1847, p. 123)
Family Coccomyxaceae (Chodat) G. M. Smith (1933, pp. 350, 366)
Family Tetrasporaceae (Nägeli) Klebs orth. mut. Wille, *in* Warming (1884, p. 23)
Syn.: Gloeochaetaceae Bohlin (1901, p. 25), *nomen nudum;* Chaetopeltidaceae (Borzi) West orth. mut. Wille (1909b, p. 98)
Family Chaetopediaceae Skuja (1948, p. 121)
Suborder **Chlorodendrineae** Fritsch (1935, p. 130)
Family Chlorodendraceae Oltmanns (1904, p. 136)
Family Chlorangiaceae Lemmermann (1915, p. 25)
Order ZYGNEMATALES Borge et Pascher (1913, p. 1, as Zygnemales)
Syn.: Conjugales (De Bary) Rabenhorst orth. mut. G. M. Smith (1920, p. 183); Mesotaeniales Fritsch, *in* West (1927, p. 225); Desmidiales Krieger (1933, p. 173), *nomen nudum*
Suborder **Zygnematineae** Papenfuss, nom. nov.
Syn.: Euconjugatae (Fritsch) Fritsch (1935, p. 311)
Family Mesotaeniaceae Oltmanns (1904, pp. 52, 53)
(According to the current Code, the nomenclature of this family starts with Ralfs, 1848.)
Family Zygnemataceae (Meneghini) Kützing orth. mut. Engler (1898, p. 11)
Syn.: Spirogyraceae Palla (1894, pp. 234, 235, as Spirogyraceen)
Family Mougeotiaceae Palla (1894, pp. 234, 235, as Mougeotiaceen)
Syn.: Mesocarpaceae (De Bary) Wittrock orth. mut. Wille, *in* Warming (1884, p. 29); Temnogametaceae West et West (1897, p. 37)
Family Gonatozygaceae (West et West) Fritsch, *in* West (1927, pp. 239, 240)
Syn.: Archidesmidiaceae Blackman et Tansley (1902, p. 189)
Suborder **Desmidineae** (Fritsch) Fritsch orth. mut. Papenfuss
(According to the current Code, the nomenclature of this suborder starts with Ralfs, 1848.)
Family Desmidiaceae Kützing (1833b, p. 591) ex Ralfs orth. mut. Stizenberger (1860, p. 27)
Syn.: Eudesmidiaceae Blackman et Tansley (1902, p. 189, p.p.)
Order ULOTRICHALES Borzi (1895, p. 348, as Ulothrichiales)
Syn.: Chaetophorales Wille (1901, p. 13); Protococcales (Meneghini) Kirchner orth. mut. Engler (1892, p. 9, p.p.); Pleurococcales Chodat (1909, p. 149); Chroolepoidales Chodat (1909, p. 155); Microsporales Bohlin (1901, pp. 19, 25); Cylindrocapsales Prescott (1951, pp. 66, 109); Ulvales Blackman et Tansley (1902, p. 136)
Family Ulotrichaceae Kützing orth. mut. Rabenhorst (1868, pp. 298, 360)
Syn.: Stichococcaceae Bohlin (1901, p. 19)
Family Microsporaceae Bohlin (1901, pp. 19, 25)
Family Cylindrocapsaceae Wille, *in* Warming (1884, p. 30)
Family Chaetophoraceae Harvey orth. mut. Stizenberger (1860, p. 34)
Syn.: Aphanochaetaceae Oltmanns (1904, pp. 197, 240); Herposteiraceae (Hasen) West (1904, p. 70); Protodermaceae Kützing (1849, p. 471)
Family Pleurococcaceae Klebs (1883, p. 342)
Family Chlorosphaeraceae Klebs (1883, p. 343)
Family Coleochaetaceae (Nägeli) Pringsheim (1860, p. 32, as Coleochaeteen)
Family Chaetosphaeridiaceae Blackman et Tansley (1902, p. 143)
Family Chaetosiphonaceae (Huber) Blackman et Tansley (1902, p. 142)
(To judge from the classical account of Huber, 1892, it is not improb-

able that future work will show that this family or some of its members actually belong in the Siphonocladales, a group with which he had allied them.)

Family Trentepohliaceae Hansgirg (1886, p. 85)

Syn.: Chroolepidaceae Rabenhorst (1868, pp. 287, 300, 371); Mycoideaceae (van Tieghem) De Toni (1888, p. 447); Hansgirgiaceae (De Toni) De Toni (1889, p. 262); Ctenocladaceae Borzi (1895, p. 353); Phycopeltidacées Marchand (1895, p. 14)

?Family Microthamniaceae West (1904, p. 89)

Family Wittrockiellaceae Wille (1909a, p. 222)

Family Coelodiscaceae Jao (1941, p. 294; see also 1947, p. 255)

Family Schizomeridaceae G. M. Smith (1933, p. 452)

Family Monostromaceae Kunieda ex Suneson (1947, p. 245)

Family Ulvaceae Lamouroux orth. mut. Dumortier (1822, p. 72)

Syn.: Capsosiphonaceae Chapman (1952, p. 55)

Order SPHAEROPLEALES (Fritsch) Prescott (1951, p. 110)

Family Sphaeropleaceae Kützing (1849, p. 362)

Order OEDOGONIALES Blackman et Tansley ex West (1904, p. 55)

(According to the current Code, the nomenclature of this order starts with Hirn, 1900.)

Family Oedogoniaceae (Thuret) De Bary orth. mut. Stizenberger ex Hirn (1900, p. 1)

Order SCHIZOGONIALES West (1904, p. 56)

Syn.: Prasiolales Fritsch, *in* West (1927, p. 164)

Family Prasiolaceae (Rabenhorst) Borzi orth. mut. Blackman et Tansley (1902, p. 138)

Syn.:, Schizogoniaceae Chodat (1902, p. 341, as Schizogoniacées); Blastosporaceae Jessen orth. mut. Wille (1909b, p. 73)

Order CHLOROCOCCALES Marchand orth. mut. et emend. Pascher (1915, p. 2)

Syn.: Protococcales (Meneghini) Kirchner orth. mut. Engler (1892, p. 9, p.p.) (See Silva and Starr, 1953, on the nomenclature of *Chlorococcum*.)

Family Chlorococcaceae Blackman et Tansley (1902, p. 95)

Syn.: Planosporaceae West (1916, p. 209); Chlorochytriaceae (West) Setchell et Gardner (1920, p. 146); Endosphaeraceae Klebs (1883, p. 344); Nautococcaceae Korshikov (1926, p. 491)

Family Chlorellaceae (Wille) Brunnthaler (1913, p. 86)

Syn.: Micractiniaceae (Brunnthaler) G. M. Smith (1950, p. 232)

Family Dictyosphaeriaceae (De Toni) West (1916, p. 190)

Family Characiaceae (Nägeli) Wille, *in* Warming (1884, p. 23)

Syn.: Characiochloridaceae Skuja (1948, p. 99), *nomen nudum*

Family Characiosiphonaceae Iyengar (1936, p. 317)

Family Gomontiaceae Bornet et Flahault ex De Toni (1889, p. 389)

(This family is placed in the order Chlorococcales on the strength of Kylin's [1935] observations. It has been pointed out to me by Dr. J. Proskauer and Dr. R. H. Thompson [personal communications] that *Gomontia* may possibly be intimately connected with such forms as *Kentrosphaera*, *Excentrosphaera*, and *Chlorochytrium*.)

Family Protosiphonaceae Blackman et Tansley (1902, p. 115)

Family Hydrodictyaceae (S. F. Gray) Dumortier orth. mut. Cohn (1880, p. 289)

Syn.: Pediastraceae Wille, *in* Warming (1884, p. 23)

Family Coelastraceae (West) Wille (1909b, p. 64)

Family Botryococcaceae Wille (1909b, p. 32; see Blackburn, 1936)

Family Oöcystaceae Bohlin (1901, pp. 17, 25)

Syn.: Glaucocystidaceae Bohlin (1901, p. 25), *nomen nudum;* Eremosphaeraceae (Wille) Brunnthaler (1913, p. 86); Selenastraceae (Blackman et Tansley) Fritsch, *in* West (1927, p. 127)

Family Scenedesmaceae Oltmanns (1904, p. 183)

Order CLADOPHORALES West (1904, p. 56)
Family Cladophoraceae (Hassell) Cohn (1880, p. 289)
Syn.: Pithophoraceae Wittrock (1877, p. 47)
Family Arnoldiellaceae Fritsch (1935, p. 246)
Family Anadyomenaceae Kützing orth. mut. Hauck (1884, p. 420)
Syn.: Microdictyaceae (De Toni) Setchell (1929, p. 584)
Order SIPHONOCLADALES (Blackman et Tansley) Oltmanns (1904, p. 134)
Syn.: Valoniales Pascher (1931, p. 327), *nomen nudum*
Family Valoniaceae Nägeli (1847, p. 154)
Family Siphonocladaceae Schmitz (1879a, p. 20)
Syn.: Apjohniaceae Setchell (1929, p. 584), *nomen nudum*
Family Boodleaceae (Børgesen) Børgesen (1925, p. 19)
Order SIPHONALES Wille, *in* Warming (1884) orth. mut. Blackman et Tansley (1902, p. 114)
Syn.: Codiales Setchell (1929, p. 584); Caulerpales Setchell (1929, p. 584); Pascher (1931, p. 327); Feldmann (1946, p. 753), *nomen nudum;* Eusiphonales Feldmann (1946, p. 753)
Family Derbesiaceae (Thuret) Kjellman (1883, p. 316)
Syn.: Halicystidaceae G. M. Smith (1930, p. 227; see also 1944, p. 69)
Family Dichotomosiphonaceae Chadefaud ex Feldmann (1946, p. 753)
Family Caulerpaceae Greville ex Kützing orth. mut. Cohn (1880, p. 288)
Family Bryopsidaceae Bory orth. mut. De Toni (1888, p. 449)
Family Codiaceae (Trevisan) Zanardini (1843, table opposite p. 171)
Syn.: Udoteaceae (Endlicher) J. Agardh (1887–1888, p. 12; see also Feldmann, 1946, p. 752); Siphonaceae Greville orth. mut. Harvey (1849, p. 190); Spongodiaceae Lamouroux orth. mut. De Toni (1888, p. 449)
Order DASYCLADALES Pascher (1931, p. 328, fn. 37)
Family Dasycladaceae Kützing orth. mut. Stizenberger (1860, p. 32)
Syn.: Acetabulariaceae (Endlicher) Hauck (1884, p. 421)

Phylum Charophycophyta

Characterization: Members of this isolated group of only seven living genera have erect, whorled, equisetoid, haploid, branched thalli that grow by means of a conspicuous dome-shaped apical cell and are attached by multicellular, branched rhizoids. By transverse division, the apical cell cuts off segments proximally. Each segment divides transversely into an upper nodal and a lower internodal cell. The internodal cell elongates greatly but undergoes no further septation. The nodal cell divides by vertical and curved walls to form a nodal tissue, certain peripheral cells of which become apical cells and give rise to a whorl of laterals of limited growth, the "leaves." The "leaves" are likewise differentiated into nodes and internodes and may be simple or branched. Indeterminate branches when formed, are produced in the axils of the laterals of limited growth.

The internodal cells of the axes and of the short laterals may or may not be ensheathed by a layer of cortical filaments that are produced by the basal nodes of the whorl of short branches. Some grow upward and ensheath the basal half of the internodal cell next above, others grow downward and cover the upper half of the internodal cell below. The cortical filaments grow by means of an apical cell and are also differentiated into nodal and internodal cells.

Young and small cells are uninucleate, whereas the large internodal cells become multinucleate by amitosis. The cells contain many small discoid chloroplasts which lack pyrenoids. As far as known, the pigment complex does not differ from that of other green plants, and food is stored as starch. The wall consists of an inner cellulosic and an outer gelatinous layer of unknown composition. In many species the thallus becomes calcified.

Vegetative multiplication is of common occurrence. Secondary protonemata may develop from the primary rhizoid or the primary protonema or the nodes of plants that have passed through a period of hibernation. Adventitious long branches may develop from the nodes of hibernating plants or parts that have become detached. Frequently, tuberlike organs of vegetative propagation are formed on the rhizoids or at the nodes of buried parts of the long branches.

Sexual reproduction is oögamous. The plants may be monoecious or dioecious. The oögonia and antheridia are produced at the nodes of the primary laterals of limited growth.

The antheridia are much more complex than those of other thallophytes. The antheridial initial divides by two intersecting longitudinal and a median transverse wall. Each of the octants so formed then divides by two periclinal walls. The eight peripheral cells, known as the shield cells, constitute the antheridial wall, the middle series of cells form what is known as the manubrium, and the innermost eight cells constitute the primary capitulum. Through the elongation of the manubrium cells and the enlargement of the capitulum cells the manubria become laterally separated from one another in the mature condition. The shield cells and the manubrium cells do not undergo division during the further development of the antheridium. Through division each primary capitulum produces six secondary capitulum cells which may or may not produce tertiary and quaternary capitula. The secondary capitula, but at times also those of lower and higher order, cut off initials which give rise to branched or unbranched septate spermatogenous filaments, each cell of which eventually forms a single, elongated, anteriorly biflagellate sperm.

The oögonia are like those of thallophytes in being single-celled and at first naked structures. During their development the cell below the oögonium produces five corticating filaments that invest the oögonium. These filaments remain undivided except at their apices, where each cuts off by transverse division one or two coronal cells. The single living family (Characeae) is divided into two subfamilies on the basis of the formation of one (Charoideae) or two (Nitelloideae) tiers of coronal cells. Only one egg is formed in each oögonium. In the mature condition the cortical filaments are spirally twisted (clockwise in all living species, counterclockwise in some fossil forms) about the oögonium.

Meiosis occurs during germination of the zygospore. At first there is produced a protonema, from the primary branch of which the mature plant arises as a lateral branch.

The living Characeae are essentially freshwater in occurrence. Many of the fossil forms were marine in distribution (Peck, 1934, p. 101).

History: The first published record of the designation *Chara* in its present sense apparently is that by the herbalist Dalechamps (1587, p. 1070) who gave it as the popular name of an *Equisetum*-like aquatic plant used by the inhabitants of Lyons to scour plates and other utensils. Vaillant in 1721 formally erected the genus *Chara.* During the following one hundred and fifty years these plants had an extremely checkered systematic history. Many of the early botanists regarded them as species of *Equisetum* or *Hippuris.* Linnaeus (1753) considered *Chara* a genus of algae. Adanson (1763, p. 472) placed it in family 56, Ara (aroids) of the flowering plants. Others, as for example De Candolle (1805, p. 584), associated the genus with the Naiadaceae.

In 1815 Richard (*in* Bonpland and Humboldt) proposed (as a *nomen nudum*) the family Characeae and regarded it as belonging to the angiosperms. Many early botanists, however, such as C. Agardh (1824), who established the genus *Nitella,* Wallroth (1833), Endlicher (1836), Kützing (1843, 1849), and others, had no hesitation in according these plants a place among the algae. On account of the spirally arranged ensheathing filaments of the oögonium, Wallroth (1833) erected for them (and a number of unrelated genera) the order Gyrophykea (one of four which he recognized in the algae), and this name was later used for the group by Rabenhorst (1847).

For a long time a great deal of misunderstanding existed regarding the nature of the reproductive organs of these plants and this more than anything else was responsible for the differences of opinion among early botanists as regards the systematic position of the group. Some authors, as for example De Jussieu (1789), regarded the antheridium as an anther and the oögonium as a pistil and consequently placed these plants among the phanerogams. The first to disagree with such an interpretation of the reproductive organs were Wallroth (1815) and Bischoff (1828), although neither of them understood their true nature.

Vaucher (1821), Kaulfuss (1825), and Bischoff (1828) studied the germination of the zygospore and thereby threw light on one phase of the reproduction of these plants. The function of the antheridium remained doubtful until Thuret in 1840 (see also his paper of 1851) discovered that flagellated sperms were produced in it. Braun (1852, 1853), Pringsheim (1863a, 1863b), Sachs (1874) and De Bary (1875) contributed further to the knowledge of the structure of the thallus, the development of the reproductive organs, and the germination of the zygospore, and De Bary (1872) studied in detail the process of fertilization. Oehlkers in 1916 produced convincing evidence that the thallus is haploid, meiosis occurring at the germination of the zygospore. (The belief of Tuttle [1926] that the plants are diploid, with meiosis occurring during the early development of the sex organs, appears to be based upon inaccurate observation.)

In addition to contributing a great deal to knowledge of the structure of the thallus and the reproductive organs, Braun in a long series of publications, especially those from 1849 onward, laid the foundation upon which the present classification of the Charophycophyta is based. At the time of his death he had in an advanced stage of preparation a monograph of the species of the world, which was completed by Nordstedt (see Braun and Nordstedt, 1883). In more recent times important contributions to the taxonomy of the group have been made especially by Migula (1890–1897, 1925), Groves and Bullock-Webster (1920, 1924) and Zaneveld (1940). Wood (1952) has given a list of the described species. In addition to the family Characeae, to which are referred all the living species as well as certain fossils, Peck (1946) recognizes three fossil families—Clavatoraceae, Trochiliscaceae, and Sycidiaceae. Mädler (1953) divides the fossil charophytes into three orders and a total of six families as follows: Sycidiales, with the family Sycidiaceae; Trochiliscales, with the family Trochiliscaceae; Charales with the families Palaeocharaceae, Clavatoraceae, Lagynophoraceae, and Characeae.

Although knowledge of the Charophyceae has progressed far beyond the stage when there was disagreement as to whether these very ancient plants were flowering plants, vascular crytogams, or nonvascular crytogams, a great deal of uncertainty still exists as to the exact phylogenetic position of the group. Cohn (1872a, 1872b, 1880) placed them as an order, Phycobryae, in the Bryophyta, to which phylum they were also referred by Bennett (1878, 1879), who apparently was not aware of Cohn's classification, and by various other botanists of the last century and by Ily as recently as 1913.

Current opinion is divided on whether the Charophyceae belong with the green algae or constitute an autonomous phylum, and, if so, whether this phylum belongs in the algae or occupies a position higher than the thallophytes.

Harvey (1849, p. 2), De Bary (1872, p. 238), and Sachs (1875, p. 278) were the first to consider the Charophyceae as forming a group removed from both the thallophytes and the bryophytes. They were followed by Migula (1890–1897), who erected the phylum Charophyta. Migula thought that both the Bryophyta and Charophyta probably had evolved from green algae but had developed along different lines. Many botanists, including a large number of students of the Charophyceae, agree with Migula in regarding the assemblage as constituting a distinct phylum, although it is not always clear from their writings whether they consider this phylum as belonging with the algae (thallophytes) or not. Groves and Bullock-Webster (1920, p. 1) remark: "The Charophyta are a small group of Cryptogams, and occupy a peculiarly isolated position, having no clear affinity with any other plants." Oltmanns (1922a, p. 457) says that he at times was doubtful whether he should include the group in his book on the algae.

Fritsch (1935, pp. 447, 465–466) although admitting (p. 447) that "the sex organs, and in particular the antheridium, though quite unparalleled among the algae, are equally unique when considered in relation to other groups of plants," nevertheless places the group as an order in the Chlorophyceae. Smith, who omitted them from the first edition (1933) of his *Fresh-water Algae of the United States* later (1938, 1950) considered them as constituting a separate class among the green algae.

Although the Charophyceae differ from green algae in a number of features, the most important single character which removes them from this group or, for that matter, perhaps from all thallophytes lies in the structure of the antheridium. As a primary and integral part of its development, this organ cuts off an outer series of sterile cells, the shield cells, which function as a protective layer to the later produced inner fertile cells. Since the exposed nature of the reproductive organs remains as one of the few clear-cut characters whereby thallophytes may be separated from plants of a higher evolutionary level, it may thus even be questioned, as have Migula, Oltmanns, and many others, whether the Charophyceae should be classified as algae.

In this connection it is of interest to consider Goebel's (1930) ingenious interpretation of the antheridium. He regards it as a compound structure consisting of eight congenitally fused short branches, each composed of three cells —an apical cell (corresponding to a shield cell) and a segment cell which has divided into two cells, the basal of which has become a capitulum cell and the other a manubrium cell.

On this interpretation of Goebel each cell of the spermatogenous filaments of the compound antheridium is an antheridium, as in many algae. It should be remembered, however, that in many plants above the level of thallophytes (e.g., bryophytes) the sperms are also produced in individual cells and yet the antheridia are not considered compound structures. It may be emphasized, furthermore, that the method of initiation of the eight short branches through longitudinal division of an initial cell does not conform to the usual method of branch initiation in the Charophyceae. But even if Goebel's interpretation should be correct, the fact remains that a reproductive structure is formed in which the fertile cells are protected by a primarily produced sterile covering.

Fritsch retains the Charophyceae in the Chlorophyceae largely because they have green plastids, produce starch, are haploid, and the Nitelleae have a simple vegetative organization; and he suspects that, if the fossil record were known, all transitions to the green algae would be found. It is quite probable that the Charophyceae evolved from the Chlorophyceae. But this is probably true also of other green plants above the level of the algae and, if all the intermediate types had persisted or were known from fossils, it would be impossible to separate the angiosperms from the green algae. The presence in the Charophyceae of green plastids, their storage of starch, and the fact that they are haploid can hardly be considered valid criteria for retaining them among the Chlorophyceae.

The classification below is adapted from the systems of Pia (1927), Peck (1946), and Mädler (1953).

Phylum CHAROPHYCOPHYTA Papenfuss (1946, p. 218)
  Syn.: Charophyta Migula (1890, p. 60)
    Class Charophyceae G. M. Smith (1938, p. 127)
        Order CHARALES Lindley (1836, p. 414, as "alliance")
          Syn.: Sycidiales Mädler (1952, p. 14); Trochiliscales Mädler (1952, p. 14)
              Family Palaeocharaceae Pia (1927, p. 90)
              Family Characeae Richard ex C. Agardh (1824, p. xxvii)
                Syn.: Lagynophoraceae Stache (1880, not seen, cited from Mädler, 1953)
              Family Clavatoraceae Pia (1927, p. 91)
              Family Trochiliscaceae Karpinski orth. mut. Peck (1934, p. 104)
              Family Sycidiaceae Karpinski orth. mut. Peck (1934, p. 116)

Phylum Euglenophycophyta

Characterization: This phylum comprises both green and colorless, naked, and often spirally twisted unicellular, flagellated, or rarely palmelloid organisms with a complex vacuolar system. In some forms (certain species of *Euglena*) the periplast is soft and the individuals thus show marked metaboly; in others (*Phacus*) it is rigid and the cells consequently do not change in shape. Depending upon the genus, the individuals usually possess one or two or occasionally three flagella that arise from the invaginated anterior end of the cell, the reservoir. The available information on the structure of the flagella of members of this phylum has been summarized by Vlk (1938), Brown (1945), Pitelka (1949), Pringsheim and Hovasse (1950), and Jahn (1951). The flagella are apparently provided with a single row of cilia along their entire length (but see the review by Pringsheim and Hovasse, 1950). Certain of the colorless forms, the Peranemaceae, are equipped for the ingestion of particulate food as contrasted with the green and saprophytic species, which apparently are unable to ingest solid food. In the green species the pigment complex consists of chlorophyll *a*, chlorophyll *b*, beta-carotene, and several unidentified xanthophylls (Strain, 1951, p. 253). Typically, food is stored in the form of the polysaccharide paramylum. No coccoid or filamentous types have become known in this phylum. The ordinary method of reproduction is by cell division. In some forms cysts are formed, the contents of which divide into a number of cells. Various instances of gametic union have been reported but none of these is entirely convincing.

History: The early history of the classification of the euglenids is inextricably linked with that of many other groups of microorganisms, or Infusoria as they were named by Ledermueller in 1763 (according to Kent, 1880–1881, p. 14). Hence, in reviewing the classification of the euglenids the history of the entire complex must be taken into account and the steps traced that led finally to their separation as an autonomous phylum.

Although a few representatives of the Euglenophycophyta had already been described before the end of the eighteenth century, especially by O. F. Müller (1786) in his *Animalcula infusoria* . . .(the first comprehensive work on the Infusoria), it was Ehrenberg who in 1838 in his volume *Die Infusionsthier-*

chen als vollkommene Organismen laid the foundation upon which the structure of knowledge of the euglenids rests. Ehrenberg erected for them the family Astasiaea, which he placed along with several other families, comprising unicellular and colonial forms such as volvocines, dinoflagellates, desmids, diatoms, and amoebae, in his "Polygastrica anentera," the gutless stomach animalcules. Dujardin (1841) showed that the "Polygastrica anentera" were not perfect miniature replicas of the Metazoa, pointing out among other things that the so-called stomach of these beings was a vacuole. He proposed a system of classification based primarily on the various means of locomotion. His third order (p. 270) comprised Infusoria ". . . pourvus d'un ou plusieurs filaments flagelliformes servant d'organes locomoteurs.—Sans bouche." It received a number of flagellated forms such as monads, volvocines, euglenids, and dinoflagellates. By uniting these organisms in a single group, Dujardin became the founder of the assemblage for which Cohn (1853, p. 273) later proposed the name Flagellata.

Siebold (1848, 1849) extended the observations of Dujardin and in conformity with Schleiden and Schwann's new cell theory pointed out for the first time that the Infusoria of Ehrenberg were single-celled beings. He abandoned Dujardin's group since he believed that the flagellated organisms were either plants or animals and there were no intermediates. Siebold erected a class Rhizopoda for the nonflagellated (amoeboid) members of this complex and placed it along with the amended class Infusoria (which included among others the euglenids) in a major group for which he adopted (with altered circumscription) the designation Protozoa of Goldfuss (1820, p. 57). Siebold excluded from his group Protozoa organisms that were unable to change their body form through contraction and expansion, such as the volvocines, desmids, and diatoms, which he regarded as plants. He was inconsistent in this, however, for he retained the peridinians as a family of animalcules in the Infusoria.

Following Siebold's establishment of the unicellular nature of the Flagellata, little of major importance to our knowledge of the group (as circumscribed by Siebold) was published until the appearance of the papers by Cienkowski (1865a, 1865b, 1870), who made the first detailed observations on the life histories of various members of the group and brought light and clarity into the chaotic state of affairs as regards knowledge of the reproduction of these organisms.

In 1878 appeared the first part of Stein's classical work on the natural history of the Flagellata. Stein regarded the Flagellata (including the Volvocaceae), in agreement with Dujardin, as belonging to the Infusoria (that is, as animals), since they possessed flagella, nuclei, and contractile vacuoles, apparently overlooking the fact that a nucleus and a contractile vacuole had previously been shown to be present in the motile reproductive cells of certain typical algae. He gave an excellent historical review of the advances in knowledge of these organisms up to the time of his writing and his illustrations of many of them still rank among the best that have been produced of the forms in question.

Comprehensive treatises covering much the same field were published shortly afterward by Kent (1880–1881) and Bütschli (1883–1887). Both these authors also gave excellent reviews of the history of the group in the broad sense.

In proclaiming that some of Ehrenberg's Infusoria were plants rather than animals, Siebold (1848) started a long-continuing dispute as regards the nature of many of the flagellated microorganisms. At first botanists were not particularly disturbed by these beings but in the course of time more and more of them became involved in the argument. By 1850, zoologists had already conceded that desmids and diatoms were plants but few of them were prepared to relinquish the flagellates, including the Volvocaceae. Haeckel (1866) attempted to resolve the problem by erecting for the flagellates and various other microorganisms a kingdom Protista, which he considered intermediate between plants and animals. Although the concept of a separate kingdom Protista was for a time accepted by some biologists, it was later found untenable and has been abandoned.

A major advance toward an understanding of the morphology and the interrelationships of the flagellatas, with special reference to the euglenids, was made by Klebs in 1883. Those biologists (Carter, 1856; Bergmann and Leuckart, 1852, pp. 132–133; Cienkowski, 1870, p. 426; Hofmeister, 1867, p. 29; Schmitz, 1882, p. 13, fn. 2) who had held that the euglenids, especially the green ones, were algae had usually related them to the Palmellaceae. Since this family encompassed a very heterogeneous assemblage of organisms such as *Protococcus* (at times referred to a separate family Protococcaceae), members of the Chlamydomonadaceae and Tetrasporaceae as now understood, and a number of other types, Klebs decided to study the structure and reproduction of various members of the Palmellaceae in order to obtain a sound basis for their comparison with the euglenids. He found that the euglenids differed from the Palmellaceae in such important points as the structure of the limiting membrane of the cell, the structure of the anterior end of the cell, the storage products, and the method of division of the cell. Consequently, Klebs concluded that the Palmellaceae were typical algae and that the Euglenaceae constituted a sharply defined group which bore no relationship to typical algae but perhaps was related, by way of the Peranemeae, to the ciliates in the Infusoria. This possible alliance was sufficiently remote, however, to justify recognition of the Euglenaceae and Peranemeae as an assemblage distinct from the ciliates. He suggested that the old designation Flagellata be employed for this group and was of the opinion that probably the monads should also be retained in the Flagellata. In excluding the Euglenaceae from the algae, Klebs was not particularly perturbed by their possession of chloroplasts since he erroneously believed that these structures were comparable to the cells of *Zoochlorella* in *Paramaecium bursaria*.

Klebs (1883) also presented a systematic arrangement of the genera and species of the family Euglenaceae, which served as the basis of later classifications of the assemblage. He divided the family into the two groups Euglenae and Astasiae, the Euglenae receiving primarily photosynthetic forms whose cells contained an eyespot and which went into a state of rest before dividing, and the Astasiae receiving saprophytic forms which lacked plastids and an eyespot and divided while in a motile state.

Klebs believed that certain other organisms, typified by the genus *Peranema*, represented a second natural group in the euglenid alliance. Among other distinguishing features, the members of this group possessed an oral apparatus.

In a later monograph, Klebs (1892) maintained that the argument whether the Flagellata were thallophytes or protozoa had lost significance and that it was best to look upon them as a group intermediate between plants and animals and one from which various other microorganisms had evolved. At this time, he divided the Flagellata into the five subgroups Protomastigina, Polymastigina, Euglenoidina, Chloromonadina, and Chromomonadina. The Euglenoidina he divided much as he had in 1883 except that he elevated the group Astasiae to the rank of family and he now definitely accepted the Peranemeae as a third family in the assemblage.

As a group of plants, the Flagellata were treated by Senn (1900) in Engler and Prantl's *Pflanzenfamilien*. He divided the Flagellata into seven subgroups as follows: Pantostomatineae, Protomastigineae, Distomatineae, Chrysomonadineae, Cryptomonadineae, Chloromonadineae, and Euglenineae.

In accordance with the classification of Klebs (1892), but in conformity with botanical nomenclature, Senn divided the Euglenineae into the three families Euglenaceae, Astasiaceae, and Peranemaceae. In 1903 (*in* Engler, 1903), he treated the Flagellatae as a division and the seven groups named above as orders. In his treatment of the euglenids in Pascher's *Süsswasser-Flora* . . . , Lemmermann (1913) accepted the three families proposed by Klebs.

Pascher in 1931 (p. 322) formally recognized the Euglenineae as an autonomous phylum of plants, the Euglenophyta. Smith (1933) established the family Colaciaceae for the genus *Colacium* and later (1938) created for it the order Colaciales. According to Jahn (1951) the removal of *Colacium* to a group of its own is well warranted.

The three families (Euglenaceae, Astasiaceae, Peranemaceae) that comprise the Euglenales are largely separated on the basis of method of nutrition although morphological characters (especially plastid structure, presence or absence of pyrenoids and nature of flagellar apparatus) are also utilized (cf., Pringsheim, 1948a; Jahn, 1951). The family Euglenaceae includes all the chlorophyll-containing genera and those colorless forms that appear to be derived from green species. The Astasiaceae are saprophytic and the Peranemaceae are holozoic. It is generally agreed by students of the group that the classification of the Euglenales is artificial but for practical reasons the separation into three families has been adhered to pending further knowledge of the complex. The autonomy of *Astasia* and certain other colorless (saprophytic) forms is especially doubtful (cf., Pringsheim, 1948b, 1952).

The order Colaciales embraces the single chlorophyll-containing genus *Colacium*. The individuals are nonmotile in the vegetative phase and are surrounded by a gelatinous sheath affixed to components of the freshwater zooplankton. Usually the individuals produced by division secrete a stalk of their own and these stalks remain attached to the stalk of the parent cell. As a result of repeated cell division there is thus formed a dendroid colony with the cells at the terminations of the dichotomously branched stalk system.

As a group, the Euglenophycophyta constitute a highly specialized and seemingly isolated assemblage with no clear alliance to other flagellated organisms. The literature on the phylum may be traced through the bibliographies of Fritsch (1935), Jahn (1946, 1951), Pringsheim (1948a), and Pringsheim and Hovasse (1950).

A synoptic arrangement of the orders and families follows.

Phylum EUGLENOPHYCOPHYTA Papenfuss (1946, p. 218)
Syn.: Euglenophyta Pascher (1931, p. 322)
Class EUGLENOPHYCEAE G. M. Smith (1933, pp. 4, 607)

Order EUGLENALES Engler (1898, p. 7, as "Reihe")
Syn.: Euglenocapsales Pascher (1931, p. 326), *nomen nudum*, based on *Euglenocapsa* Steinecke (1932); Euglénomonadales Chadefaud (1950a, p. 789)
Family Euglenaceae Stein orth. mut. Klebs (1883, p. 296)
Syn.: Eutreptiidae Hollande (1942, p. 168); Distigmidae Hollande (1942, p. 168); Euglenocapsaceae Pascher (1931, p. 326), *nomen nudum*
Family Astasiaceae Ehrenberg orth. mut. Senn (1900, pp. 174, 177)
Family Peranemaceae Klebs orth. mut. Senn (1900, pp. 174, 178)
Syn.: Menoidiidae Hollande (1942, p. 168)
Family Rhynchopodaceae Skuja (1948, p. 233)
Family Rhizaspidaceae Skuja (1948, p. 235)
Order COLACIALES G. M. Smith (1938, p. 148)
Family Colaciaceae G. M. Smith (1933, p. 612)

Phylum Chrysophycophyta

This phylum (as Chrysophyta) was established by Pascher in 1914 (cf. also Pascher, 1921) to encompass the three classes Xanthophyceae, Chrysophyceae, and Bacillariophyceae. Although the Bacillariophyceae appear to be only remotely allied to either the Xanthophyceae or the Chrysophyceae, a good deal of evidence is at hand that points to a close relationship between the latter two classes (Pascher, 1914, 1921, 1932, 1937).

The more important features of correspondence between the three classes as stressed by Pascher (1914, 1921, 1924, 1937, pp. 155–173) and other authors are: (1) storage of leucosin or oil as food reserves in members of all three classes; (2) formation of a distinctive type of endoplasmatic spore (cyst) with a usually silicified wall of two pieces; (3) possession by the vegetative cells of some Xanthophyceae (*Ophiocytium, Tribonema*) of a wall of two pieces comparable to that of the diatom frustule and that of the cysts of all three classes; (4) growth in length of the cell wall by the deposition of thimblelike segments or intercalary bands in certain members of all three classes.

Although the pigmented members of these three groups usually have yellow-green or golden-brown chromatophores and it has consequently been assumed that they possess similar pigment complexes, it is now known that there are some significant differences (Strain, 1951, p. 253). The three classes are considered separately below.

CLASS XANTHOPHYCEAE

Characterization: This class is comprised of forms which in the vegetative condition are: (1) unicellular, naked, and terminally biflagellate, excepting *Nephrochloris* which appears to be uniflagellate; (2) unicellular and amoeboid; (3) unicellular, nonmotile, and in the form of gelatinous aggregates of various shapes and sizes (palmelloid types); (4) unicellular, nonmotile, provided with a firm cell wall, and usually attached by a short mucilaginous stalk (coccoid types); (5) simple or branched septate filaments which may or may not be attached; or (6) vesicles or nonseptate branched filaments.

In the flagellated species and in the zoöspores of the nonflagellated members of the class, the two flagella are of unequal length and the longer flagellum is beset with cilia. The majority of the species are pigmented, being yellow-green owing to a preponderance of carotenoid pigments. Depending upon the species, the cells have one to many plastids which are usually of a discoid shape. The pigment complex consists of chlorophyll *a*, chlorophyll *e* (in *Tribonema*), beta-carotene, and xanthophyll. Pyrenoids are only rarely present and are of the naked type. Reserve food is stored as oil or leucosin. Rarely certain species of a genus are colorless. These forms, and also some of the pigmented species, ingest solid food or are saprophytic.

The majority of the species are uninucleate; a few are multinucleate. Where present, the cell wall is composed of pectic compounds, and it frequently consists of two equal or unequal overlapping pieces.

Multiplication is by cell division, akinetes, aplanospores, or zoöspores. Cysts with a silicified wall composed of two pieces have been observed in a number of species (cf. Pascher, 1937, pp. 71–78). Sexual reproduction has been observed with certainty (cf. Pascher, 1937, pp. 150–154) only in *Tribonema* (Scherffel, 1901, p. 149), *Botrydium* (Rosenberg, 1930; Moewus, 1940) and *Vaucheria*. *Vaucheria* is oögamous, *Tribonema* is isogamous, and *Botrydium* is isogamous or anisogamous (Moewus, 1940).

History: Despite the fact that at least one member of this class has been known since the time of Linnaeus (1753), who described *Ulva granulata* (=*Botrydium granulatum*), the bulk of our knowledge of the group has been acquired in the course of the present century, mainly through the efforts of Pascher. The distinguishing characteristics of the class remained unrecognized until the latter part of the past century. Owing to their greenish color, the few species which had become known previous to 1899 were regarded as Chlorophyceae.

Alexander Braun in 1855 (p. 49) recognized certain features of correspondence between *Ophiocytium, Sciadium,* and *Tribonema;* but it was Borzi who in 1889 (see also 1895, p. 199) first convincingly pointed to the alliance of several genera which had been placed in widely separated families of the Chlorophyceae. He erected an order Confervales for these algae and credited it with the three families Sciadiaceae, Confervaceae, and Botrydiaceae. In his work of 1895 Borzi considered the Confervales as comprising nine genera, all of which are still regarded as belonging to the Xanthophyceae. These forms were brought together by Borzi mainly on the basis of three characters: (1) they possessed discoid, yellowish-green plastids; (2) they did not store starch; and (3) their zoöspores had only one flagellum (as he believed).

Some years later, Bohlin (1897a) published a significant study of certain cytological characters of members of the Confervales, pointing out that the two overlapping pieces that form the lateral wall of the cells have a layered structure, that the wall is not composed of cellulose but of a pectic acid derivative, that the plastids contain a preponderance of yellow pigments and that the storage product is not starch (as Borzi had already established) but a fatty substance. In this paper Bohlin also described a remarkable amoeboid flagellate (*Chloramoeba*) which recalled the zoöspores of *Conferva sensu* Lagerheim (= *Tribonema*). He regarded it as the progenitor of the genera comprising the Confervales. In a footnote (p. 48) Bohlin remarked that *Chloramoeba* at times possessed two flagella—one much shorter than the other. In a later paper Bohlin (1897b) described *Chloramoeba* in some detail. It was found that if the cell lay in a certain position, two flagella—one much shorter than the other—could be observed in the majority of instances, that the cells possess two to six discoid plastids of a yellow-green color, and that the assimilatory product is stored as oil.

Two years later, Luther (1899) described another remarkable genus (*Chlorosaccus*) belonging to this complex. This genus was palmelloid in habit, its zoöspores were provided with two flagella of unequal length, and the cells contained several yellow-green, discoid plastids. In connection with his work on *Chlorosaccus* Luther also investigated the zoöspores of *Tribonema* and *Botrydiopsis* and made the important discovery that the zoöspores of these genera likewise possessed two unequal flagella instead of one flagellum as had been believed. This character was thus found to exist in several genera of the Confervales showing various levels of thallus specialization—flagellated, palmelloid, coccoid, and filamentous types.

In evaluating the phylogenetic implications of the facts contributed by Borzi, Bohlin, and himself, Luther arrived at the far-reaching conclusion that the characters whereby these algae differed from the Chlorophyceae were of such magnitude that it was no longer possible to retain them in this alliance. Consequently, he erected for them a separate class which he named Heterokontae. Luther's class, interestingly enough, corresponded very closely to Borzi's Confervales, except that he included in it the newly erected order Chloromonadales (as exemplified by *Vacuolaria*), as well as the genera *Chloramoeba* and *Chlorosaccus*. The Chloromonadina, as typified by *Vacuolaria*, had previously been established as an autonomous group of flagellates by Klebs (1892). It is now known that the Chloromonadales were misplaced in the Heterokontae.

The views of Luther as regards the autonomy of the Heterokontae were quickly adopted by a number of students of the algae, including especially Blackman (1900), Bohlin (1901), Blackman and Tansley (1902), Oltmanns (1904), West (1904), and Heering (1906). Heering gave a comprehensive treatment of the forms represented in the flora of Schleswig-Holstein and a full historical review of the class. He also pointed to (as Blackman, 1900, p. 671, had previously done) the striking parallelisms in thallus types between the Heterkontae and the Chlorophyceae.

Blackman (1900, p. 674) brought attention to the fact that *Vaucheria* appeared to be the only "green" alga outside the Heterokontae which had chlorophyll possessing the same characters as in members of the Heterokontae and wondered what the phylogenetic significance of this would prove to be. A year later, Bohlin (1901) removed the Vaucheriaceae to the Heterokontae and established for the family the order Vaucheriales. The transfer was made on the basis of the same pigment reaction he had obtained in *Tribonema*, the presence of discoid plastids, the storage of food as oil, and the observation by Walz (1866–1867, p. 134, pl. 12, fig. 4) that the sperms had two unequal flagella.

Blackman and Tansley (1902) followed Bohlin in the inclusion of *Vaucheria* in the Heterokontae and, what is important in the light of Mangenot's (1948) recent corroborative conclusion, they also removed the Phyllosiphonaceae from the Chlorophyceae to the Heterokontae, presumably on account of the storage of oil as a food reserve in this family.

Following the pioneering studies of Borzi, Bohlin, and Luther, numerous workers, but more especially Pascher, have contributed materially to our knowledge of the Xanthophyceae. In 1912 (b) Pascher elaborated upon the earlier systems of classification of the group and in accordance with the morphology of the thallus established orders which paralleled certain chlorophycean orders. He erected the order Heterochloridales to receive the flagellated members, the Heterocapsales for the palmelloid types, the Heterococcales for the coccoid genera, the Heterotrichales for the filamentous forms, and the Heterosiphonales for the siphonous representatives. As mentioned above, Pascher in 1914 and 1921 brought the Xanthophyceae in alliance with the Chrysophyceae and Bacillariophyceae.

In 1925 (a) Pascher gave a treatment of the class in his *Süsswasserflora Deutschlands...* At this time he established the order Rhizochloridales to receive the amoeboid forms. More recently Pascher (1937–1939) has produced, as a volume in the second edition of Rabenhorst's *Kryptogamen-Flora von Deutschland ...*, a monumental work of 1092 pages on the morphology and taxonomy of the known Xanthophyceae of the world. In this work Pascher recognized some 89 genera of which he alone authored 60.

In 1930 Allorge proposed the designation Xanthophyceae as a substitute for Heterokontae, and since this appellation conforms to the majority of class names of algae in connoting color and in terminating in –phyceae, it has met with favor in many quarters.

Significant evidence supporting Pascher's (1914, 1921) conclusions of a relationship between Xanthophyceae and Chrysophyceae was furnished in 1931 and 1938 by Vlk who established that the biflagellate motile cells of Xanthophyceae agreed with those of Chrysophyceae in that the long flagellum is of the tinsel type, being beset with two rows of delicate cilia, whereas the short flagellum lacks cilia.

Further facts favoring this alliance were brought to the foreground by Pascher in 1932. He pointed out that the bivalved endogenously produced cysts which he had discovered in certain Xanthophyceae in 1930 (1930a, p. 406, fig. 3c; 1930c, pp. 332–335, fig. 17; see also Pascher, 1937, pp. 71–78, figs. 56–63) were similar to the bivalved cysts characteristic of the Chrysophyceae.

Of especial interest is the abundant evidence brought forth in recent years indicating that the classical *Vaucheria* actually belongs in the Xanthophyceae rather than in the Chlorophyceae (Seybold, Egle, and Hülsbruch, 1941; Chadefaud, 1945; Strain, 1948; Koch, 1951). It will be recalled that Bohlin (1901) and Blackman and Tansley (1902) had placed *Vaucheria* in the Xanthophyceae. In general, however, phycologists have preferred to retain the genus in the order Siphonales of the green algae. Egerod (1952, p. 336) has assembled the facts in support of the inclusion of the Vaucheriales in the Xanthophyceae, the most important of which are: (1) the unequal length of the flagella of the sperm (Pringsheim, 1855, p. 142; Walz, 1866–1867, p. 134, pl. 12, fig. 4; Woronin, 1869, p. 156; Strasburger, 1887, p. 396; Koch, 1951); (2) the ciliated condition of the shorter flagellum of the sperm (Koch, 1951); and (3) a pigment complex comparable to that of Xanthophyceae (Seybold, Egle, and Hülsbruch, 1941; Strain, 1948). It is to be noted, however, that *Vaucheria* is reported as possessing only chlorophyll *a* whereas *Tribonema,* the only other member of the class whose green pigment has been analyzed (Strain, Manning and Hardin, *in* Strain, 1951, p. 247 and table 1), possesses chlorophyll *a* and *e*.

In 1948 Mangenot produced evidence for the removal of *Phyllosiphon* from the Chlorophyceae to the Xanthophyceae, where Blackman and Tansley (1902) had once accorded it a position.

The following classification of the Xanthophyceae is largely based on that of Pascher (1937–1939).

Class XANTHOPHYCEAE Allorge (1930, p. 230)
Syn.: Heterokontae Luther (1899, p. 17)
Order HETEROCHLORIDALES Pascher (1912b, p. 10)
Syn.: Series Chloramoebales Fritsch, *in* West (1927, pp. 300, 301); Xanthomonadales Chadefaud (1950a, p. 790)

Family Chloramoebaceae Luther (1899, p. 19)
Syn.: Heterochloridaceae Pascher (1925a, p. 22)
Order RHIZOCHLORIDALES Pascher (1925a, p. 26)
Family Rhizochloridaceae Pascher (1925a, p. 26)
Family Stipitococcaceae Pascher ex G. M. Smith (1933, p. 144)
Family Chlorarachniaceae Pascher (1937, p. 251)
Family Chlamydomyxaceae Hieronymus, *in* Engler (1897, p. 570; cf. Hieronymus, 1905, p. 156)
Syn.: ?Myxochloridaceae Pascher (1937, p. 256)
Order HETEROCAPSALES Pascher (1912b, p. 13)
Family Chlorosaccaceae Bohlin ex Blackman et Tansley (1902, p. 217)
Syn.: Heterocapsaceae Pascher (1912b, pp. 13, 21)
Family Malleodendraceae Pascher (1937, p. 301)
Order HETEROCOCCALES Pascher (1912b, p. 14)
Syn.: Mischococcales Fritsch, *in* West (1927, pp. 300, 302); Xanthococcales Chadefaud (1950a, p. 790)
Family Pleurochloridaceae Pascher (1937, p. 333)
Syn.: ?Halosphaeraceae Oltmanns (1904, p. 181); cf. Pascher (1925a, p. 41; 1939, p. 910)
Family Chlorobotrydaceae Pascher (1925a, p. 48)
Syn.: Gloeobotrydaceae Pascher (1938, p. 632)
Family Botryochloridaceae Pascher (1938, p. 661)
Family Gloeopediaceae Pascher (1938, p. 696)
Family Mischococcaceae Pascher (1912b, p. 14)
Family Characiopsidaceae Pascher (1938, p. 718)
(Pascher [1938, pp. 718, 800–812] includes *Harpochytrium* in the Characiopsidaceae. Wille [1900, p. 371] had proposed, as a *nomen nudum*, the family Harpochytriaceae for this genus. According to Jane [1946] *Harpochytrium*, as to type, may have to be removed to the fungi.)
Family Chloropediaceae Pascher (1938, p. 812)
Family Trypanochloridaceae Geitler (1935, p. 146)
Family Centritractaceae Pascher (1938, p. 830)
Family Sciadiaceae Borzi (1889, p. 68)
Syn.: Chlorotheciaceae Bohlin (1897a, p. 48); Ophiocytiaceae Wille (1909, p. 49)
Order HETEROTRICHALES Pascher (1912b, p. 18)
Syn.: Tribonematales Pascher (1939, p. 915); Confervales Borzi (1889, p. 68), not including *Conferva* L. (cf. Silva, 1952, p. 271); Xanthotrichales Chadefaud (1950a, p. 790)
Family Heterotrichaceae Pascher (1939, p. 916)
Family Tribonemataceae West orth. mut. G. M. Smith (1933, p. 157)
Syn.: Confervaceae *sensu* Borzi (1889, p. 69); non Confervaceae (S. F. Gray) Dumortier (1822, pp. 71, 96)
Order HETEROCLONIALES Pascher (1939, p. 991)
Family Heterodendraceae Pascher (1937, p. 992)
Family Monociliaceae West (1916, p. 414)
Syn.: Heterocloniaceae Pascher (1931, p. 324)
Order VAUCHERIALES Bohlin (1901, p. 14)
Syn.: Heterosiphonales Pascher (1912b, p. 21); Botrydiales Pascher (1939, p. 1023); Xanthosiphonales Chadefaud (1950a, p. 790)
Family Botrydiaceae Rabenhorst (1863, p. 219)
Syn.: Hydrogastraceae (Endl.) Rabenhorst orth. mut. De Toni (1889, p. 527)
Family Phyllosiphonaceae Frank orth. mut. De Toni (1888, p. 449)
Family Vaucheriaceae (S. F. Gray) Dumortier (1822, p. 71)

CLASS CHRYSOPHYCEAE

Characterization: This class embraces forms which are attached or free-floating, unicellular, colonial, or filamentous. The unicellular species may be naked or provided with a wall—usually of unknown composition but in some instances known to be composed of pectin and rarely also containing cellulose—or the naked cell may be enclosed in a capsule (lorica) which is open at one end. In many, if not all, the Mallomonadaceae and in *Aurosphaera* (Chrysosphaerales) siliceous scales are embedded in the pectic wall and the scales may bear delicate, hinged silicified needles. In the Coccolithophorineae and in *Achrosphaera* (Chrysosphaerales) the pectic wall contains discoid bodies of calcium carbonate (coccoliths) which in some instances are provided with spinelike processes. In the Silicoflagellatophycidae the naked cell contains an internal skeleton consisting of a framework of variously arranged siliceous rods.

The unicellular forms are either flagellated, or are consistently rhizopodial, or occur as gelatinous aggregations of cells (palmelloid types) or as nonmotile cells enclosed by a wall (coccoid types). Depending on the species, the flagellated cells have one, two equal (isokont), two unequal (heterokont), or one short and two long flagella. As far as known (Petersen, 1918, 1929; Vlk, 1938) the flagellum of the uniflagellate Chrysomonadales is of the tinsel type whereas in the isokont Isochrysidales one of the flagella is of the tinsel type and in the heterokont Ochromonadales the long flagellum is of the tinsel type. The structure of the flagella in the triflagellate Prymnesiales has not yet been determined.

The filamentous forms are simple or branched and have a firm cell wall which, at least in *Phaeothamnion*, is known to be composed of cellulose.

The majority of the Chrysophyceae are photosynthetic. Some are colorless and are either saprophytic or engulf solid food. Some of the pigmented forms also ingest solid food. Food is stored as leucosin, a substance of unknown chemical composition (probably a carbohydrate), and oil. The cells usually contain only one or two chromatophores which are parietal in position, and in some instances naked pyrenoidlike bodies are present. The pigmented species have a golden-brown color owing to a preponderance of carotenes and xanthophylls. As far as known the pigment complex consists of chlorophyll *a*, beta-carotene, lutein, and fucoxanthin (Strain, 1951, p. 253).

Contractile vacuoles are of common occurrence either in the vegetative stages or in the reproductive cells of species representative of all the orders.

The ordinary method of reproduction is by vegetative cell division. Some species also produce zoöspores. Sexual reproduction appears to be of extremely rare occurrence and is isogamous. Up to the present a union of gametes has been observed with certainty only in *Ochrosphaera* (Schwarz, 1932) and *Dinobryon Borgei* (Skuja, 1950). The report by Schiller (1926) of a fusion of gametes in *Dinobryon sertularia* is not entirely convincing and the observations by Mack (1951) with respect to *Chrysolykos* require confirmation. Many of the species are known to produce cysts.

The cysts constitute one of the most distinctive features of the class. They were first observed by Cienkowski (1865b) and have since been studied in a large number of species by Scherffel (1911, 1924), Conrad (1927, 1928), Doflein (1923), Pascher (1924, 1932) and others. These resting stages are formed endoplasmatically and have a wall consisting of two pieces which are usually of a different size. The larger piece is formed first and is composed of cellulose which is impregnated with silica; and the outer surface is often elaborately sculptured. The smaller piece is ordinarily in the form of a plug which seals from the inside the terminal opening left in the larger piece. The plug usually contains little or no silica and is dissolved at germination of the cyst or is separated from the wall around the pore. These cysts contain almost all the original protoplasm of the cell and leucosin, and at germination the contents ordinarily divide to form a number of motile cells which escape through the pore.

History: Hydrurus foetidus (Villars) Trevisan is the first member of this class to have been described with sufficient accuracy to be recognized by later investigators. It was described by Villars in 1789 as *Conferva foetida*. C. Agardh in 1824 (p. xviii) erected the genus *Hydrurus*. It was not until the latter part of the nineteenth century, however, that the relationship of *Hydrurus* with the Chrysophyceae was established by Klebs (1892, pp. 283–285, 420–427) and others. Because of its brown color, the genus had for a long time been classified with the Phaeophyceae (cf. Hansgirg, 1886; De Toni, 1895).

Long before *Hydrurus* had been recognized as a member of the Chrysophyceae, a number of other genera of the class had become well known as animals. The first of these (e.g., *Syncrypta, Synura, Uroglena, Dinobryon*) were described by Ehrenberg who established the family Dinobryina for *Dinobryon* and *Epipyxis* (cf. Ehrenberg, 1838).

Stein (1878) not only added to knowledge of the genera of Ehrenberg but described and illustrated several new genera belonging to this complex, including the genus *Chrysomonas* (= *Chromulina* Cienkowski, 1870). Stein was the first to recognize the interrelationship of the majority of the forms known at the time of his writing. He placed the genera in the two families Dinobryina (*Dinobryon, Epipyxis*) and Chrysomonadina (p. 152), to the latter of which he referred (p. x) ten genera, eight of which are still regarded as representative of the Chrysophyceae.

Bütschli (1883–1887) appears to have had little appreciation of the significance of Stein's classification for he placed the genera in a number of widely separated families of flagellates. Only in his assigning of *Monas, Dinobryon, Epipyxis,* and *Uroglena* to a family Heteromonadina, characterized by flagella of unequal length, did he attain a natural grouping.

The greatest advance during this early period in the delimitation of the group as a natural assemblage was made by Klebs (1892, pp. 394–427). He regarded the genera known in his time (including *Dinobryon* and *Epipyxis*) as constituting a single family Chrysomonadina in his newly established group Chromomonadina (which also included as a second family the Cryptomonadina). Klebs remarked (p. 278) that one could refer to the Chromomonadina as chrysophytes, a designation which was later formally adopted by Pascher (1914) as the phyletic name for the chrysomonads, heterokonts, and diatoms.

Klebs clearly recognized the salient features which characterized the group: (1) the golden-brown color of the organisms; (2) the characteristic storage products leucosin (named by him, 1892, p. 395) and oil in both the pigmented and the colorless members; (3) the three types of flagellation—one, two unequal flagella, or two more or less equal ones; and (4) the formation of endoplasmatic cysts of a unique type such as had been observed in a number of forms since they were first seen by Cienkowski (1865b).

Although various authors (e.g., Schmitz, 1882; Rostafinski, 1882; Hansgirg, 1886; De Toni, 1895) before the turn of the century had regarded some of the Chrysophyceae as algae (usually as Phaeophyceae), general acceptance of them as a group of plants begins with the works of Engler (1898) and Senn (1900).

In agreement with the classification of Engler, Senn divided the chrysomonads according to the number and length of the flagella into three families: Chromulinaceae (with one flagellum), Hymenomonadaceae (with two equal or more or less equal flagella), and Ochromonadaceae (with two unequal flagella).

A very significant advance in the classification of the chrysomonads was made by Pascher in 1910. He elevated the three groups (families) recognized by Engler and Senn to the rank of order (Chromulinales, Isochrysidales, Ochromonadales) and segregated the genera into seven families. (At this time Pascher also erected an order Phaeochrysidales which included organisms with two laterally inserted flagella; this group was subsequently shown to belong to the Cryptophyceae.)

In various later contributions Pascher (1912a, 1913a, 1914, 1925b, 1931) elaborated upon his classification of this group. In addition to his three original orders, he established among others the orders Rhizochrysidales, Chrysocapsales, Chrysosphaerales, and Chrysotrichales to receive the amoeboid, palmelloid, coccoid, and filamentous types, respectively. As is true of the Xanthophyceae, the bulk of our knowledge of the Chrysophyceae has been acquired during the past forty years, mostly through the investigations of Pascher. At the time of his death in 1945 he was engaged with a monograph on the group, which was to have appeared as a volume in Rabenhorst's *Kryptogamen-Flora*. . . Through his death phycology has lost its foremost student of the Chrysophyceae and the present gap in organized knowledge of this group of algae may remain unfilled for a long time. For an autobiography and bibliography of Pascher, see Pascher (1953).

In addition to Pascher, various authors (Lohmann, 1902; Scherffel, 1911, 1924, 1927; Petersen, 1918, 1929; Doflein, 1922, 1923; Schiller, 1925a, 1925b, 1930; Conrad, 1914, 1926, 1927, 1928, 1933; Kamptner, 1928; Gemeinhardt, 1930; Vlk, 1938; Huber-Pestalozzi, 1941; and others) have made significant contributions to knowledge of the Chrysophyceae during the present century. Petersen (1918, 1929) and Vlk (1938) have investigated the structure of the flagella. Scherffel (1911, 1924), Korshikoff (1929), Pascher (1916a, 1917, 1930b) and others have brought to light abundant evidence pointing to a relationship between various colorless flagellates and certain pigmented Chrysophyceae. Huber-Pestalozzi (1941) has contributed a great deal to knowledge of the freshwater planktonic forms but his work is of less value than it might have been because of the omission of a bibliography.

Brief mention should be made of the main steps in the growth of knowledge concerning the Coccolithophorineae and the Silicoflagellatophycidae which are now generally regarded as Chrysophyceae but have an interesting history of their own.

COCCOLITHOPHORINEAE

The history of our knowledge of these organisms begins with Ehrenberg (1836, 1839) who discovered in cretaceous deposits large numbers of circular and elliptic carbonate disks, which he believed had an inorganic origin.

New information as to the origin of these bodies was not forthcoming until the survey work in the North Atlantic preparatory to the laying of the first cable between Europe and America. Huxley and Wallich found in the ooze brought up from the sea bottom many carbonate bodies that resembled the disks of Ehrenberg. Huxley (1858), like Ehrenberg, believed the disks had an inorganic origin, and because of their resemblance to *Protococcus* cells he named them coccoliths.

In addition to many coccoliths, Wallich (1860a, 1861) also found in the ooze spherical bodies to whose surface adhered such coccoliths. He regarded the spherical bodies as cells of living organisms and the chalk disks as part of the skeleton of the cells. The isolated coccoliths occurring in the ooze represented, in his opinion, the remains of disintegrated cells. Wallich called the cells coccospheres and thought they were developmental stages of Foraminifera.

A few years later, Wallich (1865, p. 81, fn.; 1869) announced that he had obtained living coccospheres in surface waters of the sea. But it was not until 1877 that he proposed a generic name (*Coccosphaera*) for his coccospheres and credited the genus with two species.

Wallich and various early authors believed that these organisms were colorless. J. Murray (1891, p. 257) and Haeckel (1894, p. 110) considered them algae, although they had no adequate foundation for their belief. G. Murray and Blackman (1898) observed that the coccospheres contained a yellow-green pigment and thus furnished the first proof of their algal nature. They believed that the cells possessed a single chromatophore, but it was later shown by Lohmann (1902) and others that two plastids were present.

On the basis of a study of living material from the Mediterranean, Lohmann (1902) gave the first monographic treatment of the group, together with an account of the history of the complex up to the time of his writing. He was the first to observe that the cells were provided with one (as he believed) or two equal flagella. (Schiller, 1925a, p. 42, later found that all the flagellated species possess two equal flagella.)

Lohmann (1902, p. 125) concluded that the Coccolithophorineae shared more characters with the chrysomonads than with any of the other large groups of flagellates, and he had little hesitation in placing them in this group. Since the name *Coccosphaera*, proposed for the first genus by Wallich, was preempted by *Coccosphaera* Perty, Lohmann (p. 93) substituted the very appropriate generic name *Coccolithophora* and erected the family Coccolithophoridae, by which designation the group as a whole has since been known.

Although Lohmann was aware of the long known freshwater genus *Hymenomonas* Stein (1878), which also forms calcium carbonate plates on the cell surface, he failed to recognize it as a member of the Coccolithophorineae. The relationship between this genus and the marine representatives of the group was first pointed out by Conrad (1914).

The majority of more recent students of the Coccolithophorineae (e.g., Conrad, 1926; Kamptner, 1928; Schiller, 1930; Huber-Pestalozzi, 1941) have regarded the group as belonging to the Chrysophyceae, although Schiller (1930, p. 147), in agreement with Schussnig (1925), considers them sufficiently distinct from other Chrysophyceae to warrant placing them in a separate subclass. In agreement with Conrad (1926), Fritsch (1935) and Huber-Pestalozzi (1941), the group is here considered as representative of the order Isochrysidales, which is comprised of motile unicellular forms with two equal flagella. It should be pointed out, however, that Schiller (1926) has shown that a few genera apparently lack flagella.

The most comprehensive monograph of the group is that by Schiller (1930) which appeared as part of a volume in Rabenhorst's *Kryptogamen-Flora* . . . Although a great majority of the species are marine in occurrence, forming a very important component of the phytoplankton, a number of freshwater species have become known. The classification of the complex here adopted is essentially that of Schiller.

SILICOFLAGELLATOPHYCIDAE

This subclass includes only six clearly defined genera of marine flagellates. The first representatives of the group to be described were fossil forms that were found by Ehrenberg in 1839 in cretaceous marls from Oran and Sicily. He erected the genus *Dictyocha* for these fossils and two years later (Ehrenberg, 1841) observed the first living specimens of this genus in water from the North Sea. In subsequent years he described a large number of additional species as well as a second genus (*Mesocena*).

Ehrenberg believed these organisms to be diatoms. Haeckel (1862) placed them with doubt with the Radiolaria. The group retained its doubtful alliance with the Radiolaria until 1891 when Borgert showed, as a result of a detailed study of living specimens of *Distephanus speculum,* that they differed strikingly from Radiolaria. He observed the occurrence of brown plastids in the cells and also established for the first time that the cells owed their motility to the presence of one (*Distephanus*) or two (*Ebria*) flagella. Borgert consequently considered these organisms as an autonomous group of flagellates for which he (1891, p. 661) proposed the name Silicoflagellata.

On the basis of Borgert's findings, Haeckel in 1894 (p. 126) classified these organisms with the algae. Engler (1903) considered them (with a query) as constituting an independent phylum of thallophytes.

Lemmermann (1901a, 1901b) gave the first systematic treatment of the group and the present system is still essentially that proposed by him. Largely on the basis of skeletal structure he divided the group into two orders: (1) the Siphonotestales, which are uniflagellate and in which the skeleton is composed of hollow siliceous beams, and (2) the Stereotestales, which are biflagellate and in which the siliceous framework of the skeleton is solid. Each of these orders received a single family. Although they appeared to constitute a clearly demarked group, Lemmermann (1901b, p. 254) thought the silicoflagellates might be related to certain of the other groups of flagellates.

Pascher (1912a, p. 193) brought attention to the correspondence between the skeletons of silicoflagellates and the cysts of Chrysophyceae and hence allied these groups. With the notable exception of Schulz (1928) and Gemeinhardt (1930, 1931), who believe that the silicoflagellates constitute an autonomous class, the majority of students of the group concur with Pascher in relating them to the Chrysophyceae. Hovasse (1932) is of the opinion that the Ebriaceae (which are heterotrophic) may be more nearly related to the Radiolaria or certain Dinophyceae than to the Silicoflagellatophycidae.

The most comprehensive treatment of the group is that given by Gemeinhardt (1930) in Rabenhorst's *Kryptogamen-Flora* . . . Almost half the known species of the world are known only from fossils. In 1931 Gemeinhardt published a valuable account of the silicoflagellates collected during the German South Polar Expedition of 1901–1903.

The systematic arrangement of the Chrysophyceae presented below departs in certain respects from that of Pascher (1931). The present arrangement is a synthesis of the systems of Pascher (1931), Fritsch (1935), Huber-Pestalozzi (1941), and Smith (1950). It should be emphasized, however, that our knowledge of the Chrysophyceae is still extremely fragmentary and any systematic arrangement adopted at this time is unavoidably artificial. Thus, for instance, the orders Chrysomonadales, Isochrysidales, Ochromonadales, and Prymnesiales[2] are based largely on the possession by the component forms of one, two equal, two unequal, or one short and two long flagella, respectively, whereas differences in flagellation are not considered a valid criterion for the segregation into separate orders in the Chrysocapsales (in which the motile stages of some genera possess one and of others two flagella of equal or unequal length), Chrysosphaerales (some contain one and some two flagella of unequal length), and Chrysotrichales (some with one and some with two flagella of unequal length).

Class CHRYSOPHYCEAE (Pascher) Fritsch, *in* West (1927, p. 22)
Syn.: Chrysophyceae Pascher (1914, p. 143, as "Reihe")
Subclass CHRYSOPHYCIDAE Papenfuss, nom. nov.
Syn.: Chrysomonadineae Senn (1900, pp. iv, 152)
Order CHRYSOMONADALES Engler (1898, p. 8)
Family Chrysomonadaceae Stein orth. mut. De Toni (1895, p. 598)
Syn.: Chromulinaceae Engler (1897, p. 570); Chrysapsidaceae Pascher (1910, p. 11); Euchromulinaceae Pascher (1910, p. 15); Chromophytonaceae Hansgirg orth. mut. De Toni (1895, p. 599)
Family Oicomonadaceae Senn (1900, p. 118)
Cf. Scherffel (1911, p. 329); Pascher (1912a, p. 190)
Family Mallomonadaceae Pascher (1910, p. 31)
Family Pedinellaceae Pascher (1910, p. 8)
Syn.: Cyrtophoraceae Pascher (1911a, p. 122)
Order ISOCHRYSIDALES Pascher (1910, p. 36)
Syn.: Hymenomonadales Fritsch, *in* West (1927, p. 315)
Suborder **Isochrysidineae** G. M. Smith (1933, pp. 170, 174)
Family Isochrysidaceae Pascher (1910, p. 36)
Syn.: Syncryptaceae G. M. Smith (1933, p. 174)
Family Synuraceae G. M. Smith (1933, p. 175)
Suborder **Coccolithophorineae** Papenfuss, nom. nov.[3]
Syn.: Coccolithineae (Lohmann) Kamptner (1928, p. 23); Family Coccolithophoridae Lohmann (1902, p. 127); Class Coccosphaerales Lemmermann (1908, p. 24); Class Coccolithophorales Lemmermann (1908, p. 33); Order Coccosphaerales Haeckel (1894, p. 110)
Family Syracosphaeraceae (Lohmann) Lemmermann (1908, p. 35)
Syn.: Pontosphaeraceae Lemmermann (1908, p. 33)
Family Halopappaceae Kamptner (1928, p. 24)
Family Deutschlandiaceae Kamptner (1928, p. 27)
Family Hymenomonadaceae Senn (1900, p. 159)
Syn.: Euhymenomonadaceae Pascher (1910, p. 41); Thoracosphaeraceae (Kamptner) Schiller (1930, p. 156)
Family Coccolithophoraceae (Lohmann) Lemmermann (1908, p. 38)
Syn.: Coccosphaeraceae G. Murray et Blackman (1898, p. 439); Rhabdosphaeraceae Lemmermann (1908, p. 39); Coccolithaceae Kamptner (1928, p. 25)
Order OCHROMONADALES Pascher (1910, p. 47)
Family Monadaceae Stein orth. mut. Engler (1898, p. 7)
Syn.: Ochromonadaceae Senn (1900, p. 163); Dendromonadaceae Stein

2. Pascher (1929a, p. 271, footnote) is inclined to think that a second short flagellum may have been overlooked in *Prymnesium* (cf., however, Carter, 1937, pp. 40–43). The only other genera in the order, *Platychrysis* and *Chrysochromulina*, contain one short and two long flagella, according to Carter (1937) and Lackey (1939), respectively.

3. The classification of this suborder is based on the systems of Kamptner (1928) and Schiller (1930).

orth. mut. Engler (1898, p. 7); Euochromonadaceae Pascher (1910, p. 47); Physomonadaceae G. M. Smith (1933, p. 182, cf. Korshikov, 1929, pp. 253–261)

Family Dinobryaceae Ehrenberg orth. mut. Engler (1897, p. 570)
Syn.: Lepochromonadaceae (Pascher) Fritsch (1935, p. 555)

Order PRYMNESIALES (Fritsch) Papenfuss, stat. nov.
Syn.: Series Prymnesieae Fritsch (1935, p. 512)
Family Prymnesiaceae Conrad (1926, pp. 219–221, as Prymnésiacées)
Syn.: Chrysochromulinidae Lackey (1939, p. 138)
Family Platychrysidaceae Carter (1937, p. 47)

Order RHIZOCHRYSIDALES[4] Pascher (1925b, pp. 497, 561)
Syn.: Myxochrysidales Pascher (1931, p. 323)
Family Rhizochrysidaceae (Pascher) Doflein orth. mut. G. M. Smith (1933, p. 183)
Syn.: Chrysarachniaceae Pascher (1931, p. 323)
Family Chrysothecaceae Pascher (1931, p. 323; cf. Huber-Pestalozzi, 1941, p. 241)
Family Stylococcaceae Huber-Pestalozzi (1941, p. 242)
Family Lagynionaceae Fritsch ex Huber-Pestalozzi (1941, p. 242)
Family Myxochrysidaceae Pascher ex Huber-Pestalozzi (1941, p. 242)

Order CHRYSOCAPSALES Pascher (1912a, p. 175)
Syn.: Hydrurales Pascher (1931, p. 323)
Family Chrysocapsaceae Pascher (1912a, p. 175)
Family Naegeliellaceae Pascher (1925b, pp. 559, 561)
Family Hydruraceae (Rostafinski) Hansgirg orth. mut. De Toni (1895, p. 596)
Family Celloniellaceae Pascher (1931, p. 323)
Family Ruttneraceae Geitler (1943, p. 108)

Order CHRYSOSPHAERALES Pascher (1914, p. 143)
Syn.: Silicococcales Schiller (1925b, p. 67); Pterospermales Schiller (1925b, p. 72) *nomen nudum*; Ochrosphaerales Schwarz (1932, p. 459)
Family Chrysosphaeraceae Pascher (1914, p. 159)
Syn.: Aurosphaeraceae Schiller (1925b, p. 67)
Family Chrysostomataceae Chodat (1921, p. 83, as Chrysostomatacées)
This provisional family is probably based, according to Pascher (1925b, pp. 546–548) and Scherffel (1927, pp. 355–356), on the cysts of members of the Chrysomonadales.
Family Pterospermaceae Lohmann (1904, p. 39, as Pterospermaceen)
See the remarks of Schiller (1925b, p. 72) and Fritsch (1935, p. 550) regarding the status of this group.
Family Chrysopediaceae Pascher (1931, p. 323)
Family Stichogloeaceae Wille ex Huber-Pestalozzi (1941, p. 263)

Order CHRYSOTRICHALES Pascher (1914, p. 143)
Syn.: Cryptotrichales Pascher (1914, p. 150); Chrysothallales Huber-Pestalozzi (1941, p. 14)
Family Chrysotrichaceae Pascher (1914, p. 143)
Syn.: Nematochrysidaceae Pascher (1925b, p. 498)
Family Phaeothamniaceae (Lagerheim) Hansgirg orth. mut. De Toni (1888, p. 448)
Family Thallochrysidaceae Conrad, *in* Pascher (1914, p. 143)
Syn.: Chrysothallaceae Huber-Pestalozzi (1941, p. 14)

Subclass SILICOFLAGELLATOPHYCIDAE (Borgert) Papenfuss, stat. nov.
Syn.: Order Silicoflagellatae Borgert (1891, p. 661)

---

4. As various authors (Pascher, 1913a; G. M. Smith, 1920; Doflein, 1928, p. 461; Huber-Pestalozzi, 1941, p. 241) have remarked, this is an artificial order since the majority, if not all, the forms placed here may have been derived from or represent the nonflagellated stages of various flagellated members of the class.

Order SIPHONOTESTALES Lemmermann (1901a, p. 92)
Family Dictyochaceae Lemmermann (1901a, p. 92)
According to Gemeinhardt (1930, pp. 22, 77), Schulz established a family Cornuaceae for the monotypic genus *Cornua* Schulz (1928, p. 285), but I can find no mention of such a family in Schulz's writings.

Order STEREOTESTALES Lemmermann (1901a, p. 93)
Family Ebriaceae Lemmermann (1901a, p. 93)

APOCHROMATIC GROUPS OF UNCERTAIN SYSTEMATIC POSITION

Klebs (1892, pp. 282–283) and Senn (1900, p. 152) even in their time already suspected a relationship between certain colorless flagellates belonging to the family Monadaceae and certain pigmented chrysomonads of the family Ochromonadaceae. Subsequent work by a number of investigators (Scherffel, 1911, 1924; Pascher, 1916a, 1917, 1930b; Korshikoff, 1929, among others) have amply substantiated the suspicions of Klebs. It is generally agreed today that many of the colorless species are derived from pigmented species or are perhaps only colorless forms of pigmented species. These forms not only agree with their pigmented counterparts in the general morphology of the cell, type of flagellation, and kind of food reserve but they also produce cysts of the same kind. Consequently the families Oicomonadaceae and Monadaceae have in the preceding treatment of the Chrysophyceae been accorded positions in the Chrysomonadales and Ochromonadales, respectively.

Klebs (1892) recognized two groups of colorless flagellates, the Protomastigina and the Polymastigina. Senn (1900) distributed these colorless forms among the three groups Pantostomatineae, Protostomatineae, and Distomatineae. As mentioned above, some of these organisms (e.g., members of the Monadaceae and Oicomonadaceae) have been shown to be colorless Chrysophyceae. The systematic position of the majority of the forms, however, is still uncertain. Since at least some of them possess features that suggest an affinity with the Chrysophyceae, the three groups recognized by Senn and many subsequent authors are here appended to the Chrysophyceae.

The history of these groups is briefly considered below.

Pantostomatineae: This group was established by Kent (1880–1881, pp. 211, 229, as Flagellata-Pantostomata) to embrace a heterogeneous assemblage of flagellated organisms that engulf food by pseudopodia. Its present circumscription is that given by Senn (1900, pp. 110, 111). He assigned to it a number of genera, belonging to the two families Holomastigaceae and Rhizomastigaceae, which share certain features, especially the absence of a differentiated oral apparatus, solid food being engulfed by pseudopodia that form at any point on the cell surface. Since the time of Senn, treatments of the group have been given by Lemmermann (1907–1910, 1914), Doflein (1928), Fritsch (1935) and Huber-Pestalozzi (1941). The complex comprises only the two families assigned to it by Senn.

Family Holomastigaceae (Lauterborn) Senn (1900, p. 112)
Family Rhizomastigaceae Bütschli orth. mut. Senn (1900, p. 113)

Protomastigineae: This group was established by Klebs (1892, p. 293) to include a number of families characterized by the fact that food is taken in at a specific place on the cell. The present circumscription of the assemblage is essentially that given by Senn (1900, pp. 117–118), who removed the Rhizomastigaceae (placed here by Klebs) to the Pantostomatineae and added certain families, among others the Tetramitaceae, which Klebs had placed in his group Polymastigina. Since the time of Senn, Lemmermann (1914, pp. 52–121) and Huber-Pestalozzi (1941, pp. 280–301), among others, have given treatments of the group. It is comprised of the following families.

Family Trypanosomaceae Doflein orth. mut. Lemmermann (1914, p. 64)
Family Bicoecaceae Stein orth. mut. Senn (1900, p. 121)
Family Craspedomonadaceae Stein orth. mut. Senn (1900, p. 123)
Family Phalansteriaceae Senn (1900, p. 129)
Family Bodonaceae Bütschli orth. mut. Engler (1898, p. 7)
Family Cryptobiaceae Lemmermann (1914, p. 107)
Family Amphimonadaceae Kent orth. mut. Engler (1898, p. 7)
Syn.: Spongomonadaceae Stein orth. mut. Engler (1898, p. 7)
Family Trimastigaceae Kent orth. mut. Senn (1900, p. 141)
Family Tetramitaceae Kent orth. mut. Engler (1898, p. 7; see Skuja, 1948, p. 68)
?Family Paramastigaceae Skuja (1948, p. 68)

Distomatineae: This group was first established by Klebs (1892, p. 329) as a subgroup Distomata of his group Polymastigina. The present circumscription of the Distomatineae is essentially that of Senn (1900). He removed some of the forms which Klebs had placed in the Polymastigina to the Protomastigineae, abandoned the group Polymastigina, and elevated the Distomata to a group of major rank. (See Doflein, 1928, who retains the Polymastigina and credits it with seven families, p. 620.)

The forms placed in this small group are characterized, among other features, by the double nature of the individuals—the body consisting of two halves and usually possessing two nuclei, two sets of flagella, and two oral fissures. (For a discussion on the occurrence of synzoöspores in the algae in general, including the Chrysophyceae, and a comparison of them with representatives of the Distomatineae, reference should be made to two papers by Pascher: 1929, 1939.)

All the representatives of the Distomatineae are placed in the family Distomataceae (Klebs) Blochmann orth. mut. Engler (1898, p. 7).

CLASS BACILLARIOPHYCEAE

Characterization: This class is comprised of uninucleate, diploid, unicellular and colonial, unattached (mostly free floating) or attached forms in which the inner part of the wall of the cell (known as the frustule) consists of pectin and the outer part of siliceous material. The wall is composed of two halves, one of which, the epitheca, is slightly larger and overlaps the other, the hypotheca. Each theca is in turn always composed of at least two pieces—the somewhat convex valve which is attached at its edges to the connecting band. It is the two connecting bands that overlap slightly, and together they constitute what is known as the girdle. In a number of forms the depth of the frustule is increased by the formation of one to many (depending upon the species) intercalary bands between the valves and their connecting bands.

The valves are usually elaborately sculptured whereas the ornamentation in the connecting bands is ordinarily much less conspicuous. The sculpturing is due to perforated thin areas (chambers) in the siliceous material (cf. Kolbe, 1948, pp. 4–12; Desikachary,

1952) which appear as punctae or areolae. The striae of some Pennales represent individual areolae or linear series of closely placed small areolae (punctae). With few exceptions the markings on the two valves are similar.

In many representatives of the order Pennales one or both the valves possess a complex system of slits and canals, the raphe system. Such forms are capable of independent gliding movement, apparently owing to cytoplasmic streaming.

In colonial forms the cells are connected to one another in various ways by mucilage that is secreted through pores in the valves.

Depending upon the genus, the cell contains one, two, or many yellow, olive-green, or brown chromatophores. Naked pyrenoidlike bodies are frequently present. The pigment complex consists of chlorophyll *a*, chlorophyll *c*, carotenes, and xanthophylls. Reserve food is stored as oil or leucosin.

The usual method of reproduction is by vegetative cell division. The hypotheca of a dividing cell always becomes the epitheca of one of the two daughter cells. In the course of time there is thus in the vast majority of diatoms a considerable diminution in cell size in a population. Restoration of the maximal size characteristic of a species is brought about sooner or later by the production of rejuvenescent cells, called auxospores. In the majority of species investigated auxospores are formed as the result of a sexual process and two cells are usually involved. Meiosis precedes gametogenesis. One or at most two nonflagellated gametes are produced; or in certain Centrales four flagellated male gametes are formed (Stosch, 1951a). During the process of conjugation the gametes may escape from the parent frustules and fuse with those of the other cell. The zygote (auxospore) enlarges and ultimately produces a new frustule of maximal dimensions. Some species are autogamous and various instances of apogamy are on record.

Various authors have reported the formation of small anteriorly or laterally biflagellate cells (microspores) by members of the order Centrales. For a long time the function of these cells was unknown. Stosch (1951a, 1951b) and Geitler (1952) recently produced evidence that at least in some instances they are male gametes.

Endogenous cysts with a wall consisting of two pieces, comparable to those of the Chrysophyceae and Xanthophyceae, have been observed in several members of the order Centrales.

The Bacillariophyceae are divided into two orders, Centrales and Pennales, largely on the basis of the shape and ornamentation of the siliceous shell. In most Centrales, the valves are circular, angular, or irregular in outline and are radially or otherwise symmetrical with respect to a central point. In the Pennales the valves are isobilateral, medianly zygomorphic, or dorsiventral with at most only two planes of symmetry—one passing through the longitudinal axis, the other through the transverse axis, of the valve. In some members of this order the valves possess only one of these two planes of symmetry.

Although a classification into two orders on this basis may seem to be artificial, it apparently is quite natural. In addition to the differences in the shape and ornamentation of the valves, the two orders differ in various other characters. Centric diatoms usually have many plastids, always lack a raphe and hence show no movement, produce cysts and may form motile male gametes. Pennate diatoms, on the other hand, usually have only one or two plastids, many possess a raphe and hence show movement, and do not form cysts or motile male gametes.

History: The first person who described species of diatoms in a precise enough manner to afford their recognition by later workers was O. F. Müller. In 1773 he described a species of *Gomphonema* as *Vorticella pyraria*. Among the species which he described in later years, the most important is the one which he (O. F. Müller, 1783, p. 81, fn. c; 1786, p. 54) named *Vibrio paxillifer*. Gmelin (1788, p. 3903) established the genus *Bacillaria* for Müller's *Vibrio paxillifer*, and this name was later proposed by Nitzsch (1817), and following him used for a time especially by zoologists, for the entire group of so-called rod animalcules.

The resemblance of many colonial diatoms to filamentous algae accounts for the attention that these organisms received from various early botanists, who often described species under the generic name *Conferva.* Although as far as known, De Candolle did not especially investigate members of this group, he (*in* Lamarck and De Candolle, 1805, p. 48) was the first to regard the species previously known by the name *Conferva flocculosa* as representative of a distinct genus which he named *Diatoma,* and thus furnished the name that C. Agardh (1824) adopted for the group (as Diatomeae) and by which it is now commonly known.

The most significant contributor to knowledge of this group during this early period was Nitzsch (1817). He gave the first useful illustrations of members of the class and also recognized their prismatic quality, which he considered a major character of the group. He carefully studied the multiplication of the rod-like forms by longitudinal division and pointed out, among other things, that the individuals did not lose their form after death. Nitzsch divided diatoms into two groups, animal and plant, according as they exhibited movement or not.

Until 1832 members of this class were regarded partly as animals (the motile forms) and partly as algae (the nonmotile forms), although several botanists (C. Agardh, 1817, 1824, 1830–1832; Lyngbye, 1819; and others) had no hesitation in referring the entire group to the algae. In fact, C. Agardh in 1824 established for them the order Diatomeae, one of six which he recognized in the algae. Ehrenberg (1832, and many later publications), to the contrary, regarded all diatoms as animals, without reservations, placing them in the family of rod animalcules (Bacillaria).

C. Agardh, Ehrenberg, and others grouped the desmids with the diatoms. Kützing (1833b) was the first to recognize clearly the differences between these two groups of organisms, especially as regards the nature of the cell wall. Later, in a comprehensive monograph on the diatoms, Kützing (1844) elaborated on his earlier observations on the composition of the shell and pointed out that it is composed of silica. In this monograph Kützing also concerned himself with the classification of these organisms, and on the basis of the structure of the frustule, recognized a total of nineteen families (including one comprised largely of silicoflagellates).

Thwaites (1847, 1848) was the first to observe the process of conjugation in diatoms. At first (1847) he did not comprehend the significance of his observations but in 1848 he fully suspected that these phenomena were instances of a sexual process.

In a monograph on diatoms published in 1853, Rabenhorst corrected certain of Ehrenberg's and Kützing's errors with respect to the structure of the frustule. In this publication, Rabenhorst considered the diatoms as constituting an autonomous class of algae, which had no equal among living things as regards the sharpness of characters as shown by their peculiar type of shell. Previously, however, Harvey (1836) had regarded the diatoms (including the desmids) as forming one of the four divisions into which he divided the algae.

Turpin in 1828 (b) expressed the view that the diatom shell consisted of three pieces, instead of two as had previously been believed, two valves, and a girdle. This view was adhered to until Wallich (1858, 1860b) pointed out that the girdle actually consisted of two connecting bands, one fitting over the other.

From the point of view of the distribution of these pieces at cell division, Wallich did not realize the significance of his discovery. In 1869 Macdonald and Pfitzer independently of each other pointed out that, since at division a new valve and a new connecting band are formed within each of the two connecting bands of the parent cell, one of the daughter cells is smaller than the other, which is of the same size as the parent. (That there occurs a decrease in the size of the frustule of a species at each cell division was suspected previously by Griffith and Henfrey, 1856, p. 201.) Through continued division, cells are thus formed whose dimensions are appreciably below the maximum characteristic of the species. Ultimately the cells would be too small to undergo further division and the race would perish unless a periodic reestablishment of maximal size occurred. Both Macdonald and Pfitzer considered the process of conjugation as probably providing the required rejuvenescence. This postulate gained substance through the earlier observation of Braun (1851) that the cell developing from a zygote is larger than the parent cells. Pfitzer also noted that in some instances a rejuvenating spore was produced by only one cell. Irrespective of their method of formation, Pfitzer called these spores auxospores (enlarging spores).

Two years later Pfitzer (1871) furnished abundant evidence favoring not only the concept of a reduction in the size of diatom cells through vegetative cell division but the reestablishment of the maximal size of the species through the process of auxospore formation. In this work he also gave the first detailed account of the living part of the diatom cell, the protoplast, which previously had received only slight attention, and introduced the characters presented by the plastids in the classification of these organisms.

It will be recalled that largely because of their movement certain (or all) diatoms were for a long time regarded as animals. The exact method of movement of these organisms remained a matter of conjecture for more than a hundred years after the first species were described. In a series of papers starting in 1889 O. Müller produced evidence that the movement of the cells is owing to cytoplasmic streaming along the raphe. Although the detailed mechanics of the process are not yet entirely understood, Müller's interpretation is still accepted as the most plausible explanation of the phenomenon. In 1895 Müller also published a valuable paper on the axial relations and planes of symmetry in diatoms, and coined, among others, the terms epitheca and hypotheca to denote the larger and smaller halves, respectively, of the frustule.

Klebahn in 1896, working on *Rhopalodia gibba,* a member of the order Pennales, was the first to obtain cytological results suggesting that diatoms are diploid and that meiosis occurs during gametogenesis. Further evidence of this was produced by Karsten in 1899, and in 1912 he gave convincing proof of the diploid nature of another member of the Pennales. Since that time various authors (Geitler, 1927a, 1927b, 1928; Cholnoky, 1928, 1933a; Meyer, 1929; Subrahmanyan, 1947) have confirmed the fact that the Pennales are diploid and that meiosis precedes auxospore formation. Since a conjugation of cells was not known to occur during auxospore formation in the Centrales, it was believed for a number of years (cf. Oltmanns, 1922a) that these forms, to the contrary, were haploid and that auxospore formation is an asexual process. The first person to show that the Centrales were likewise diploid and that here auxospore formation also is a sexual process (autogamy) was Persidsky (1929, 1935). His observations have been confirmed by Cholnoky (1933b) and more particularly by Iyengar and Subrahmanyan (1942, 1944), Stosch (1951a), and Geitler (1952). It would seem therefore that the Centrales and Pennales are not as remote from each other as has been supposed.

In 1897 G. Murray observed in certain marine members of the order Centrales rounded protoplasmic bodies which he interpreted as reproductive cells. Since then these so-called microspores have been observed by a number of investigators in various marine as well as freshwater Centrales. In some instances the microspores are provided with two lateral and in others with two terminal flagella of equal length. Stosch (1951a) observed with certainty only one flagellum. It has been thought that these microspores are gametes but actual proof of this was not forthcoming until Stosch (1951a, 1951b) and Geitler (1952) showed that in some species they are actually male gametes. For a review of the literature on the microspores reference should be made to the works of Karsten (1928, pp. 167–175), Fritsch (1935, pp. 633–637), Subrahmanyan (1946), and Stosch (1951a).

Utilizing a concept introduced into the classification of diatoms by Grunow in 1860, Kirchner (1878) and Schütt (1896) divided these organisms into two groups, called Circulares and Bilaterales by Kirchner (p. 41) and Centricae and Pennatae by Schütt, on the basis of the shape and symmetry relations of the valves. West (1904) elevated these two groups to the rank of order, accepting Schütt's designations, and Karsten (1928) changed the names to Centrales and Pennales. Rabenhorst (1853) was the first to consider the diatoms as constituting an independent class of algae, which he (1864) named Diatomophyceae. The currently accepted name, Bacillariophyceae, was proposed by Fritsch (1935, p. 7). Engler and Gilg (1924, p. 13) and Karsten (1928) have elevated the group to the rank of phylum (Bacillariophyta) but in general phycologists have adhered to the interpretation of Pascher (1914, 1921), who, largely on the basis of the formation of endoplasmatic cysts in certain Centrales (first correctly interpreted by Schütt in 1888) comparable to those of Chrysophyceae and Xanthophyceae, has related them to the latter two classes. The advantages of the present system of classification of the diatoms, which is based largely on the characters presented by the siliceous shell, is that it is applicable to the many fossil representatives (which are of considerable economic importance) as well as the living forms. The arrangement presented below is essentially that of Hustedt (1930).

Class Bacillariophyceae Fritsch (1935, p. 7)
Syn.: Class Diatomophyceae Rabenhorst (1864, p. 2); Order Pyritophyceae Stizenberger (1860, p. 23); Division Bacillariophyta Engler et Gilg (1924, p. 13)
Order CENTRALES (Schütt) West orth. mut. Karsten (1928, p. 201)
Family Coscinodiscaceae Kützing orth. mut. De Toni (1890, p. 915)
Syn.: Thaumatodiscaceae Cleve orth. mut. De Toni (1894, p. 1010); Melosiraceae Kützing orth. mut. De Toni (1890, p. 913); Xanthiopyxidaceae (Petit) De Toni (1890, p. 914); Discaceae Schütt orth. mut. Karsten (1928, p, 201)
Family Asterolampraceae H. L. Smith orth. mut. De Toni (1890, p. 919)
Syn.: Heliopeltaceae H. L. Smith orth. mut. De Toni (1890, p. 918); Actinodiscaceae (Schütt) Hustedt (1930, p. 56)
Family Eupodiscaceae Kützing orth. mut. De Toni (1890, p. 916)

Family Rhizosoleniaceae (Petit) De Toni (1890, p. 921)
Syn.: Soleniaceae (Schütt) Karsten (1928, p. 202)
Family Chaetoceraceae H. L. Smith orth. mut. De Toni (1890, p. 920)
Family Biddulphiaceae Kützing orth. mut. De Toni (1890, p. 910)
Syn.: Isthmiaceae Cleve orth. mut. De Toni (1890, p. 913); Hemiaulidaceae Heiberg orth. mut. De Toni (1890, p. 912)
Family Anaulaceae (Schütt) Hustedt (1930, p. 56)
Family Euodiaceae (Schütt) Hustedt (1930, p. 56)
Family Rutilariaceae Pantocsek orth. mut. De Toni (1894, p. 1020)
Order PENNALES (Schütt) West orth. mut. Karsten (1928, p. 202)
Family Diatomaceae (S. F. Gray) Dumortier (1829, p. 77)
Syn.: Fragilariaceae Kützing orth. mut. De Toni (1890, p. 905); Meridionaceae Kützing orth. mut. De Toni (1890, p. 904); Trachyspheniaceae (Petit) De Toni (1890, p. 904); Plagiogrammaceae (Petit) De Toni (1890, p. 906); Licmophoraceae Kützing orth. mut. De Toni (1890, p. 907); Striatellaceae Kützing orth. mut. De Toni (1890, p. 907); Entopylaceae Grunow orth. mut. De Toni (1890, p. 909); Tabellariaceae Kützing orth. mut. West (1904, p. 281)
Family Eunotiaceae Kützing orth. mut. Rabenhorst (1853, pp. vii, 8, 15)
Family Achnanthaceae Kützing orth. mut. De Toni (1890, p. 900)
Syn.: Cocconeidaceae Kützing orth. mut. De Toni (1890, p. 899)
Family Naviculaceae Kützing orth. mut. Rabenhorst (1853, pp. ix, 9, 36)
Syn.: Cymbellaceae Kützing orth. mut. De Toni (1890, p. 898); Gomphonemaceae Kützing orth. mut. De Toni (1890, p. 899); Amphitropidaceae (Pfitzer) De Toni (1890, p. 898); Amphipleuraceae Grunow orth. mut. De Toni (1890, p. 902); Cocconemaceae West (1904, p. 298)
Family Epithemiaceae Grunow orth. mut. De Toni (1892, p. 776)
Family Nitzschiaceae Grunow orth. mut. De Toni (1890, p. 901)
Syn.: Cylindrothecaceae (Kirchner) De Toni (1890, p. 902)
Family Surirellaceae Kützing orth. mut. De Toni (1890, p. 903)

Phylum Pyrrophycophyta

Characterization: This phylum as now delimited embraces the single class Dinophyceae which includes two somewhat dissimilar groups of largely unicellular organisms, the subclasses Desmophycidae (desmokonts) and Dinophycidae (dinoflagellates, peridinians).

The Dinophycidae comprise forms which in the vegetative condition are (1) unicellular and biflagellate,[5] (2) unicellular and amoeboid, (3) unicellular, nonmotile, and in the form of small gelatinous aggregates (palmelloid types), (4) unicellular and nonmotile, with a firm cell wall (coccoid types), or (5) in the form of multicellular attached filaments.

These diverse types share two prominent features which suggest that they constitute a related assemblage. Firstly, the flagellated species and the motile reproductive cells of the nonmotile forms exhibit what Graham (1951) calls a "dinoflagellate orientation." In them the two flagella are inserted near each other and laterally on what is known as the ventral side. One of the flagella is usually threadlike and projects backwards. At its proximal end it lies in a ventral, longitudinal groove, the sulcus. The other flagellum is ribbon-shaped and encircles the cell. It lies in a transverse or spiral groove, the girdle. The second feature common to these organisms is found in the structure of the nucleus: the chromatin is contained in threads which are distinctly beadlike and this character persists throughout karyokinesis.

Less distinctive features which the Dinophycidae share with the Desmophycidae are: (1) the possession by the photosynthetic forms of a complex of pigments which give them a greenish tan or golden brown color (where examined [Strain, 1951, p. 253]

5. *Polykrikos* is colonial and each individual in the chainlike colony is furnished with two flagella. Whether or not any of the cells are separated by transverse walls is not clear from the literature.

the pigments have been found to consist of chlorophyll *a*, chlorophyll *c*, beta carotene, and four xanthophylls, three of which, as far as we know, are peculiar to the Dinophyceae); and (2) the storage of food in the form of starch or oil.

The cells of members of the Dinophycidae are either naked or are provided, in the forms referred to as armored dinoflagellates, with a cellulose wall, the theca. (The family Amphilothaceae comprises a small number of poorly known marine genera which possess an elaborate internal skeleton that may be silicified.) In some forms the cell is adorned with cellulosic horns (e. g., *Ceratium*) or saillike processes (e. g., *Ornithocercus*) which aid in flotation. In the thecate, flagellated forms, the theca is made up of a series of articulated plates (except in members of the small family Ptychodiscaceae, in which it is homogeneous), the number and arrangement of which are important characters in classification.

As regards method of nutrition, the Dinophycidae include both photosynthetic and heterotrophic forms (saprophytes, ecto- and endoparasites, and types with holozoic nutrition).

The genera *Polykrikos* and *Nematodinium* possess nematocysts comparable to those occurring in coelenterates.

The subclass Demosphycidae includes forms which are less specialized than those belonging to the Dinophycidae. The motile stages are biflagellate (with the flagella dissimilar or showing different movements) but do not show a dinoflagellate organization. In the vegetative condition the cells are provided with a cellulose wall (except in *Desmomastix* which is naked) that consists of two valves joined by an antero-posterior suture or that splits into two valves along an antero-posterior plane when the protoplast is caused to swell. The sulcus and girdle are lacking and the two flagella are anterior in position. (The genus *Desmocapsa* is nonmotile in the vegetative condition and forms small palmelloid aggregates.) The Desmophycidae are placed in the Dinophyceae primarily on account of the structure of the nucleus. As far as known, the chromatin threads show the same mouiliform condition as is characteristic of the Dinophycidae.

The usual method of reproduction is by cell division, which in some forms is effected while the cell is motile, in others during an immobile phase. Cysts with a thick wall and abundant stored food are produced in a number of species, especially those inhabiting fresh water. The occurrence of sexual reproduction in the pyrrophycophytes has been established with certainty only in two species (Gross, 1934; Diwald, 1938).

History: ". . . and all the waters that were in the river were turned to blood. And the fish that was in the river died; and the river stank, and the Egyptians could not drink of the water of the river; and there was blood throughout all the land of Egypt." (Exodus, vii. 20, 21.)

Although the luminescent members of this group and those which, when present in large numbers, give a blood-red color to water have attracted the attention of man for centuries, the freshwater *Ceratium hirundinella* and *Peridinium cinctum* are the forms to have been described first in a sufficiently precise manner to be recognized by later workers. They were described by O. F. Müller in 1773 as *Bursaria hirundinella* and *Vorticella cincta.* These two species and a marine form which Müller described later were subsequently redescribed and illustrated by him in 1786 in his *Animalcula infusoria fluviatilia et marina* . . .

Following the publication of several papers in the proceedings of the Berlin Academy describing new genera and species and other observations upon Dinophycidae, Ehrenberg in 1838 gave the first treatment of them as a coherent group in his famed work *Die Infusionsthiere als vollkommene Organismen.* Ehrenberg (1838, p. 249) placed them, along with certain organisms which he erroneously classified with them, in his twelfth family, the Peridinaea or "Kranzthierchen" (wreath animalcules), which formed the last family in his group "Polygastrica anentera," the gutless stomach animalcules.

Ehrenberg observed the posteriorly directed flagellum but erred in usually figuring this end of the cell as the anterior end. He also failed to understand the nature of the transverse flagellum, which he interpreted as a transverse band (or at times as two transverse bands) of cilia.

That the longitudinal flagellum is directed posteriorly was first pointed out by Perty in 1852. He (1852) was also the first to call attention to the existence of naked representatives of the group.

In *Gymnodinium uberrimum* Allman in 1855 first observed the peculiar structure of the nucleus in this phylum. Carter in 1858 confirmed an earlier observation by Allman (1855) to the effect that these organisms at times formed resting stages. Furthermore, he noted the division of the protoplast of resting stages to produce new individuals, which circumstance, apparently more than the fact that some of these beings possess chlorophyll, caused him to conclude that dinophycids were plants rather than animals. Carter (1858) was also the first to establish that the wall of dinophycids, at least as far as the resting stages were concerned, is composed of cellulose.

On account of the alleged presence of a transverse band of cilia, Claparède and Lachmann (1858–1859) created a separate order Cilioflagellata for the dinophycids, and regarded them as a connecting link between the flagellates and the ciliates. To these authors goes the credit for first pointing out that the desmophycid genus *Prorocentrum* is related to the dinophycids instead of the cryptomonads where Ehrenberg (1838) had placed it.

In 1872, Allmann expressed the view that the highly modified *Noctiluca* is allied to the dinophycids. This luminescent genus had for a long time been associated with the coelenterates and in 1873 Haeckel created for it the order Cystoflagellata, but subsequent work has shown that Allman's conclusion was well founded.

In a paper devoted largely to investigations on bacteria, Warming in 1876 briefly referred to his observations on dinophycids. He announced the occurrence of cellulose in the wall of the motile stages of these organisms and thus extended the earlier findings of Carter (1858) that the wall of resting stages consists of cellulose. Warming also established that in these organisms food is stored in the form of starch and that some of them possess a pigment similar to that of diatoms. On the basis of these significant observations, Warming concluded, as Carter (1858) previously had on much less secure grounds, that the dinophycids were algae.

A new era in the study of these organisms started with the publication in 1878 and 1883 of the first and second fascicles of the third part of Stein's *Der Organismus der Infusionsthiere*. Stein not only gave the best systematic treatment that had yet been presented of the group but illustrated them abundantly and with considerable accuracy. Some of his figures still rank among the best that have been produced of the species in question. Stein regarded the Dinophyceae as animals and placed them (Stein, 1883) as a suborder, "arthrodele Flagellaten" (articulated flagellates), in his order "Flagellaten." He divided the suborder into the five families Prorocentrinen, Noctilucciden, Peridiniden, Dinophysiden, and Cladopyxiden.

During the period that Stein was studying these organisms, Bergh (1881) also published a treatise on them. He regarded them as constituting an order Cilioflagellaten which he divided into two families: the Adinida, which included the girdleless and anteriorly biflagellate *Prorocentrum,* and the Dinifera, which received the forms with "dinoflagellate" structure. The latter family he divided into the three subfamilies Dinophysida, Peridinida, and Gymnodinida. The descriptive appellations Adinida and Dinifera introduced by Bergh have been employed in one form or another in the classification of the Pyrrophycophyta down to the present.

One of the most important advances in our knowledge of the structure of the dinophycid cell since the time of Ehrenberg was made by Klebs in 1883. He established that in freshwater forms the alleged transverse band of cilia actually is a single flagellum that lies in the transverse groove. A year later (Klebs, 1884) he established that this is true also of marine forms. A second significant contribution made by Klebs (1883) was concerned with the nucleus. He described the jointed structure of the chromatin threads and recognized the systematic value of this feature. It will be recalled that Allman in 1855 had already noted this condition (an observation which appears to have been overlooked by Klebs), but it is through the work of Klebs that this peculiarity was first brought into focus.

Klebs in 1883 believed that the Dinophyceae were thallophytes but that they occupied a seemingly isolated position among them. In 1884 he was inclined to think that these organisms might be related to some of the other yellow flagellates.

Confirmation of Klebs's observations, both with respect to the single transverse flagellum and the structure of the nucleus, came forth quickly through the work of Bütschli (1885). In Bronn's *Klassen und Ordnungen des Thier-Reichs,* Bütschli (1883–1887) also gave a comprehensive treatment of the Dinophyceae, including an excellent review of the history of knowledge of the group. In consequence of the new information concerning the flagellation, Bütschli abandoned the name Cilioflagellata given to these organisms by Claparède and Lachmann and substituted the designation Dinoflagellata (whorled flagellates?) which has remained as the popular name of the assemblage. Recent observations by Deflandre (1934) indicate, ironically, that the transverse flagellum of *Glenodinium uliginosum* bears a single row of cilia.

The first formal recognition of the dinoflagellates as a group of plants came in 1890 and 1892 when Warming (1890)[6] and Engler (1892) accepted them as a subdivision of the thallophytes. They were henceforth always included in treatises on the algae or the plant kingdom as a whole.

An outstanding monograph on the structure of the cell in marine dinoflagellates was published by Schütt in 1895 as part of the results of the Plankton Expedition, and in 1896 the same author presented an excellent systematic treatment of the group, with the exception of certain forms such as *Noctiluca* and *Polykrikos* which were excluded. Schütt (1896) divided the group into three families: (1) the Prorocentraceae, which included the terminally biflagellate forms, (2) the Gymnodiniaceae, which received the athecate forms with dinoflagellate organization, and (3) the Peridiniaceae, in which he placed the thecate forms with dinoflagellate organization.

---

6. According to Warming (1890, p. V) the dinoflagellates were first accepted as algae by Petersen and himself in 1889 in their *Grundträk af Foreläsninger over systematisk botanik for medicinske og farmaceutiske studerende.*

With few exceptions (e.g., *Pyrocystis*) the Pyrrophycophyta which had become known to science previous to 1912 were flagellated forms. In that year Klebs published his significant discovery of several nonmotile unicellular organisms that at certain stages in their development clearly revealed their relationship to the dinoflagellates.

Two years later Pascher (1914) not only announced the discovery of a number of additional nonmotile types but proposed a far-reaching revision of the classification of the dinoflagellates. He erected a phylum Pyrrophyta and accredited it with the three groups Cryptophyceae[7], Desmokontae, and Dinophyceae. The Dinophyceae received, in addition to the characteristic flagellated forms with dinoflagellate organization, those nonmotile genera with *Gymnodinium*-like swarmers that had been discovered by Klebs and himself. Some of these forms had a palmelloid organization (his Dinocapsales), others had a coccoid organization (his Dinococcales), and the single representative of a third group had a filamentous organization (his Dinotrichales).

The Desmokontae included the forms which lacked a dinoflagellate organization throughout their life history. They were divided into the two orders Desmomonadales and Desmocapsales, the Desmomonadales receiving the four families Desmomonadaceae, Exuviaellaceae (*nomen nudum*), Prorocentraceae, and Dinophysiaceae and the Desmocapsales accommodating the monogeneric family Desmocapsaceae.

Knowledge of the pyrrophycophytes has progressed by great strides during the past forty years. Space permits the consideration of but a few of the many investigations that have contributed to this advancement.

For our knowledge of the parasitic dinoflagellates we are especially indebted to Chatton, who in 1920 published an extensive monograph on the morphology and taxonomy of these forms. Some of them are ectoparasites, others are endoparasites, mostly on marine metazoa. Although these species bear little resemblance to ordinary dinophyceids, their relationship to them is clearly revealed by the structure of the motile reproductive cells.

In a long series of publications, Kofoid and his associates contributed significantly to our knowledge of the motile dinophyceids. In 1921 Kofoid and Swezy produced a monograph on the unarmored forms, based mostly upon their observations of living material obtained in the vicinity of La Jolla, California. They described a number of new families and genera and presented a revision of the classification of Dinophyceae. Kofoid and Swezy did not follow Pascher (whose paper of 1914 they did not refer to) in the separation of the terminally biflagellate forms into a separate group, the Desmokontae. They regarded the Dinoflagellata as a subclass of the class Flagellata in the phylum Protozoa and treated the terminally biflagellate forms as an order Adiniferidea of this subclass. The forms with "dinoflagellate" motile cells they placed in an order Diniferidea.

With few exceptions, the genera which Pascher placed in his orders Dinocapsales, Dinococcales, and Dinotrichales were not considered by Kofoid and Swezy. In fact they regarded (p. 109) the genera described by Klebs (1912), namely, *Phytodinium, Tetradinium, Stylodinium,* and *Gloeodinium,* as more nearly related to the green algae than to the dinoflagellates.

---

7. The Cryptophyceae are now excluded from the phylum.

In 1928 Kofoid and Skogsberg published an extensive monograph upon the dinoflagellates of the "Albatross" expedition. Three new families and five new genera were described in this work.

The most extensive systematic treatises on the pyrrophycophytes are those of Lindemann, published in 1928 as a volume in the second edition of Engler and Prantl's *Pflanzenfamilien*, and of Schiller, published in two volumes between 1931 and 1933, and 1935 and 1937. Many of the currently accepted families were established by Lindemann. The volumes by Schiller appeared as part of the second edition of Rabenhorst's *Kryptogamen-Flora von Deutschland, Österreich und der Schweiz* but their scope is much more comprehensive than the title of the series suggests inasmuch as they treat of all the known living species. Valuable general accounts of the phylum have recently been given by Fritsch (1935) and Graham (1951).

The classification presented in the synopsis below is a synthesis of the systems of Pascher, Lindemann, Schiller, Fritsch, and Graham. This arrangement departs in certain major respects from Pascher's system and in conclusion it is deemed desirable to review briefly the more significant points in the evolution of this classification.

It will be recalled that Pascher (1914, 1927a, 1931) accredited the Pyrrophycophyta with the three groups Desmokontae, Cryptophyceae, and Dinophyceae. Fritsch (1935) treats the Cryptophyceae as a distinct class, which at best may be only distantly related to the other two groups. Graham (1951) has further emphasized the distinctness of the Cryptophyceae, especially as regards the structure of the nucleus, and in agreement with him they are here considered as a separate class appended to the Pyrrophycophyta.

Fritsch (1935) in agreement with many earlier workers, regards the Desmokontae and the Dinophyceae of Pascher as more closely related than is implied by Pascher's system and treats them as groups, Desmokontae and Dinokontae, belonging to a common class, the Dinophyceae.

Pascher (1914) accredited the Desmokontae with the two orders Desmomonadales and Desmocapsales. Fritsch (1935, p. 672) produces convincing reasons for placing the single genus *Desmocapsa*, upon which Pascher based the Desmocapsales, in the family Desmomonadaceae of the order Desmomonadales.

In the order Desmomonadales Pascher (1914) had placed four families, viz., Desmomonadaceae, Exuviaellaceae, Prorocentraceae, and Dinophysiaceae. In 1928 Lindemann established the order Thecatales[8] for the Prorocentraceae, leaving the order in the Desmokontae (or Adiniferae as he called this group). Pascher (1931), Schiller (1931), Fritsch (1935), and Graham (1951) have accepted this order, except that Pascher and Graham call it Prorocentrales.

Lindemann also established an order Dinophysiales for the Dinophysiaceae, added to it a second family, the Amphisoleniaceae, and removed the order to the Dinokontae (or Diniferae as he called this group). Pascher (1931), Schiller (1931), who enriched the order with two more families, and Fritsch (1935) accept the order Dinophysiales but retain these forms in the Desmokontae. Graham (1951, p. 111), however, produces well-founded arguments for referring the Dinophysiales to the Dinokontae, with which group Kofoid and Skogsberg (1928) as well as Lindemann had related it.

8. As "Klasse," but Lindemann's classes are actually all orders.

Present-day classification of the flagellated Dinophycidae is largely based on the systems of Kofoid, Lindemann, and Schiller. Whereas the Dinophyceidae were represented by two families in the arrangement of Schütt, published in 1896, they are here segregated into eight orders and a total of 38 families.

Phylum PYRROPHYCOPHYTA Papenfuss (1946, p. 218)
Syn.: Pyrrophyta Pascher (1914, p. 153)
Class Dinophyceae Fritsch (1935, pp. 8, 665)
Subclass desmophycidae (Pascher) Graham orth. mut. Papenfuss
Syn.: Desmokontae Pascher (1914, p. 149, as "Reihe"); Subdivision Adiniferae (Bergh) Lindemann (1928, p. 36); Order Adiniferidea (Bergh) Kofoid et Swezy (1921, p. 108); Subclass Desmokontae (Pascher) Graham (1951, p. 105)
Order DESMOMONADALES Pascher (1914, p. 148)
Syn.: Desmocapsales Pascher (1914, p. 149); Athecatales Lindemann (1928, p. 36)
Family Desmomonadaceae Pascher (1914, p. 149)
Syn.: Desmocapsaceae Pascher (1914, p. 149; cf. Fritsch, 1935, p. 672); Haplodiniaceae Lindemann (1928, p. 36)
?Family Adinimonadaceae Schiller (1931, p. 9)
Order THECATALES Lindemann (1928, p. 37)
Syn.: Tribe Thecatoidae Kofoid et Swezy (1921, p. 106), *nomen nudum;* Prorocentrales Pascher ex Graham (1951, p. 114)
Family Prorocentraceae Engler (1892, p. 6)
Syn.: Exuviaellaceae Pascher (1914, p. 148), *nomen nudum*
Subclass dinophycidae (Fritsch) Graham orth. mut. Papenfuss
Syn.: "Group" Dinokontae Fritsch (1935, pp. 670, 679); "Reihe" Dinophyceae Pascher (1914, p. 151); Subclass Dinokontae Graham (1951, p. 105)
Order GYMNODINIALES (Poche) Lindemann (1928, p. 39)
Syn.: Amphilothales (Kofoid et Swezy) Lindemann (1928, p. 68; cf. Zimmermann, 1930, pp. 438–440; Schiller, 1935, p. 1)
Family Pronoctilucaceae Lebour orth. mut. Lindemann (1928, p. 39)
Family Gymnodiniaceae (Bergh) Schütt (1896, pp. 1, 2)
Family Polykrikaceae Kofoid et Swezy orth. mut. Lindemann (1928, p. 46)
Family Noctilucaceae Kent orth. mut. Lindemann (1928, p. 47)
Family Warnowiaceae Lindemann (1928, p. 51)
Family Amphilothaceae Kofoid orth. mut. Lindemann (1928, p. 68)
Syn.: Gymnasteraceae Poche orth. mut. Lindemann (1928, p. 69); Gymnosclerotaceae Schiller (1935, p. 1)
Order BLASTODINIALES Schiller (1935, p. 8)
Family Paradiniaceae Schiller (1935, p. 15)
Family Blastodiniaceae Chatton orth. mut. West (1916, p. 50)
Family Syndiniaceae Chatton orth. mut. Schiller (1935, p. 53)
Family Endodiniaceae Schiller (1935, p. 61)
Family Ellobiopsidaceae Schiller (1935, p. 62)
Order DINOPHYSIALES (Kofoid) Lindemann (1928, p. 72)
Family Dinophysiaceae (Bergh) Engler orth. mut. Pascher (1914, p. 158)
Family Amphisoleniaceae Lindemann (1928, p. 77)
Family Ornithocercaceae Kofoid et Skogsberg orth. mut. Schiller (1931, p. 192)
Family Citharistaceae Kofoid et Skogsberg orth. mut. Schiller (1931, p. 255)
Order PERIDINIALES Schütt (1896, p. 1)
Syn.: Kolkwitziellales Lindemann (1928, p. 70)
Family Ptychodiscaceae (Schütt) Lemmermann (1899, p. 362)
Syn.: Kolkwitziellaceae Lindemann (1928, p. 71; cf. Schiller, 1935, p. 75)

Family Pyrophacaceae Lindemann (1928, p. 96)
Syn.: Glenodiniopsidaceae Schiller (1935, p. 80)
Family Glenodiniaceae (Schütt) Lemmermann (1899, p. 361)
Syn.: Kyrtodiniaceae Schilling (1913, p. 12); Dinosphaeraceae Lindemann (1928, p. 84; cf. Schiller, 1935, p. 99)
Family Peridiniaceae Ehrenberg orth. mut. Engler (1892, p. 6)
Syn.: Krossodiniaceae Schilling (1913, p. 30)
Family Goniaulaceae Lindemann (1928, p. 84)
Family Congruentidiaceae Schiller (1935, p. 320)
Family Protoceratiaceae Lindemann (1928, p. 83)
Family Ceratiaceae (Schütt) Lindemann (1928, p. 91)
Syn.: Heterodiniaceae Lindemann (1928, p. 95; cf. Schiller, 1937, pp. 327–432)
Family Goniodomaceae Lindemann (1928, p. 94)
Family Ceratocoryaceae (Schütt) Lindemann (1928, p. 98)
Family Oxytoxaceae (Schütt) Lindemann (1928, p. 97)
Family Cladopyxiaceae (Kofoid) Poche orth. mut. Lindemann (1928, p. 99)
Family Ostreopsiaceae Lindemann (1928, p. 96)
Family Podolampaceae (Schütt) Lindemann (1928, p. 100)
Family Lissodiniaceae Schiller (1937, p. 480)
Order RHIZODINIALES Pascher (1931, pp. 320, 326)
Family Amoebodiniaceae Pascher (1931, p. 326)
Syn.: Dinamoebaceae Pascher (1916b, p. 135)
Order DINOCAPSALES Pascher (1914, p. 151)
Family Gloeodiniaceae Pascher ex Schiller (1937, p. 482)
Syn.: Dinocapsaceae Pascher (1914, p. 158), *nomen nudum*
Order DINOCOCCALES Pascher (1914, p. 151)
Family Hypnodiniaceae Pascher (1931, p. 326), *nomen nudum*
Family Phytodiniaceae Klebs (1912, p. 443)
Syn.: ?Pyrocystaceae (Schütt) Poche orth. mut. West (1916, p. 55); Dissodiniaceae Graham (1951, p. 116), *nomen nudum*
Family Protaspidaceae Skuja (1939b, p. 116; cf. Skuja, 1948, p. 375)
Family Stylodiniaceae Pascher (1931, p. 326), *nomen nudum*
Order DINOTRICHALES Pascher (1914, p. 151)
Family Dinotrichaceae Pascher (1914, pp. 151, 158, 160; 1927a, pp. 2–15; 1931, p. 326)
Family Dinocloniaceae Pascher (1927a, p. 15; 1931, p. 326)

Classes of Uncertain Systematic Position

CLASS CRYPTOPHYCEAE

Characterization: This class embraces less than two dozen genera of highly specialized, asymmetrical, compressed, usually flagellated, pigmented or rarely colorless, unicellular organisms. The cells have a firm periplast but lack a wall. The flagella, of which there are two, are of slightly unequal length and are somewhat ribbon-shaped with a tapering end. They are usually inserted terminally but are lateral in a few forms. A few species are palmelloid and at least one monotypic genus (*Tetragonidium*) is coccoid in organization. The majority of the pigmented forms are provided with two parietal plastids of a brown, red, blue, green or bluegreen color. In rare and somewhat doubtful instances (cf. Pringsheim, 1944, p. 148) the cells appear to contain several discoid plastids. Pyrenoids and an eye-spot may or may not be present. The colorless forms are saprophytic or holozoic. In the motile genera and in the zoöspores of the immobile forms there is a superficial curved furrow which extends backward from the place of insertion of the flagella. In many genera a "gullet" extends into the protoplast from the point of insertion of the flagella. The "gullet" may or may not be lined on the side adjacent to the protoplast with trichocysts, or (in the Cryptochrysidaceae) the trichocysts may be situated in the furrow. The cells usually contain one contractile vacuole. Reserve food is deposited as starch or starchlike compounds. Many of the Zooxanthellae growing symbiotically in the tissues of radiolarians and corals are members of this class.

History: Knowledge of the Cryptophyceae begins with the year 1832, when Ehrenberg described *Cryptomonas* and *Chilomonas.* In 1838 he erected for *Cryptomonas* (and certain other forms which have since been shown to belong elsewhere) the family Cryptomonadina, and referred it to his group "Polygastrica anentera."

Dujardin (1841, p. 270) placed the cryptomonads along with a number of other flagellated organisms in his order "Infusoires pourvus d'un ou plusieurs filaments flagelliformes servant d'organes locomoteurs.—Sans bouche," for which group Cohn (1853) later proposed the designation Flagellata.

The cryptomonads retained their position in the Flagellata for a long time (Stein, 1878; Bütschli, 1883–1887; Klebs, 1892; Senn, 1900; Lemmermann, 1907–1910). Various early authors (e.g., Cienkowsky, 1870; Schmitz, 1882; Dangeard, 1889) regarded them as algae, but general acceptance of them as a group of plants begins with the year 1900 when Senn gave a treatment of them in Engler and Prantl's *Natürlichen Pflanzenfamilien.*

Klebs (1892, p. 392) circumscribed the group Flagellata in such a way that it included only the five subgroups Protomastigina, Polymastigina, Euglenoidina, Chloromonadina, and Chromomonadina. The Chromomonadina comprised, according to his system, the two families Chrysomonadina Stein and Cryptomonadina Ehrenberg. Although he placed these two families of essentially yellow-brown organisms in a common group, Klebs emphasized that the cryptomonads stood well apart from the chrysomonads. He especially drew attention to the fact (p. 420) that the cryptomonads stored starch, which was not known to occur in other Flagellata (according to his circumscription of this assemblage), and in this respect agreed with the dinoflagellates.

Klebs regarded the Flagellata as standing intermediate between plants and animals and believed they were the progenitors of various other lower organisms. He was impressed by the prominent plantlike features of many members of his group Chromomonadina and said (p. 278) that one could refer to them as chrysophytes, a designation that was later formally adopted by Pascher (1914) as the phyletic name for the chrysomonads, heterokonts, and diatoms.

In agreement with Klebs (1892), Pascher in 1911 (b) believed in an alliance between the cryptomonads and the chrysomonads, but he also pointed to the possibility of a relationship between the cryptomonads and the dinoflagellates, a view which had been held previously by Bergh (1881) and Bütschli (1883–1887, 1885). In fact, Ehrenberg in his day had placed *Prorocentrum* in his family Cryptomonadina. Pascher finally in 1914 removed the cryptomonads from the vicinity of the chrysomonads and placed them as a group, Cryptophyceae, along with the Desmophycidae and the Dinophycidae in the newly erected phylum Pyrrophyta.

Fritsch (1935), Smith (1938), Pringsheim (1944), Graham (1951), and others have accepted the class Cryptophyceae but various authors, especially Pringsheim and Graham, have been skeptical of its presumed relationship with the Dinophyceae. Graham has in fact removed the class from the Pyrrophycophyta—primarily on the basis of the difference in nuclear structure.

The following arrangement is a synthesis of the systems of Pascher (1931) and Pringsheim (1944). Pringsheim has pointed to certain weaknesses in the classification of Pascher and more recently Skuja (1948) has added to the class the new family Senniaceae and has removed the Nephroselmidaceae to the Volvocales in the green algae.

Class Cryptophyceae (Pascher) Fritsch, *in* West (1927, p. 387)
Non Cryptophyceae Thuret, *in* Le Jolis (1863, pp. 13, 25), *nomen nudum*
Order CRYPTOMONADALES Senn, *in* Engler (1903, p. 7)
Syn.: Phaeochrysidales Pascher (1910, p. 9); Phaeocapsales Pascher (1912a, p. 196); Cryptocapsales Pascher (1931, p. 325)
Family Cryptochrysidaceae (Pascher) Pascher (1931, p. 325)
Family Cryptomonadaceae Ehrenberg orth. mut. Senn, *in* Engler (1903, p. 7)
Syn.: Phaeocapsaceae De Toni (1895, p. 591); Phaeoplakaceae Pascher (1931, p. 325); Chilomonadaceae Lemmermann (1908, p. 473)
Family Cyathomonadaceae Pringsheim (1944, p. 149)
Family Kathablepharidaceae Skuja (1939b, p. 96)
Family Senniaceae Skuja (1948, p. 367)
Order CRYPTOCOCCALES Pascher (1914, p. 150)
Family Cryptococcaceae Pascher (1931, p. 325)
See the figures of *Tetragonidium* by Thompson *in* Smith (1950, p. 636).

CLASS CHLOROMONADOPHYCEAE

Characterization: This class embraces a few highly specialized unicellular, anteriorly biflagellate genera (excepting *Monomastix*, which is uniflagellate, and *Merotrichia*, which is laterally biflagellate). The cells are naked, provided with a delicate periplast, metabolic, flattened, dorsiventral, ovoid or pear-shaped, and usually possess a longitudinal groove on the ventral surface. The flagella issue from a slight depression—one is directed forwards and the other trails behind along the ventral surface. They are of the same length, except in *Thaumatomastix* and *Vacuolaria viridis*, in which the trailing flagellum is longer than the other, and in *Gonyostomum*, in which it may be shorter or longer than the other. The majority of the forms are green and are provided with numerous discoid chromatophores containing a preponderance of xanthophylls. Nothing is known about the composition of the pigment complex. Two of the genera (*Reckertia*, *Thaumatomastix*) are colorless and presumably holozoic. Food is stored as oil. An eye-spot is lacking. Contractile vacuoles are present. Some forms (e. g., *Trentonia*, *Gonyostomum*) are provided with an anterior cavity connected by a duct to the exterior and some (e. g., *Merotrichia*, *Gonyostomum*) possess trichocysts. Reproduction is by longitudinal division of the cell. Cysts with a firm gelatinous wall may be produced.

History: This small class of only seven genera was first established as an autonomous group (Chloromonadina) by Klebs (1892, pp. 292, 391–394) who referred to it the genus *Vacuolaria* Cienkowski (1870) and forms belonging to *Gonyostomum* Diesing (1866) and *Merotrichia* Mereschkowsky (1879) as currently delimited. The first species to have been described sufficiently well to be recognized by later workers is *Gonyostomum semen* which was described by Ehrenberg (1853) as *Monas? semen*. Bütschli (1884, p. 819) placed the members known at the time of his writing together with a variety of unrelated genera in his family Coelomonadina.

Formal recognition of the Chloromonadina as a group of plants begins with Engler (1898, p. 8) and Luther (1899, p. 19) who independently erected for them an order Chloromonadales. Luther placed the order in his class Heterokontae.

Senn (1900, pp. 170–173) maintained the chloromonads as a separate group in the Flagellata and gave a systematic treatment of the complex. Some of the genera which he referred to the group have since been shown to belong elsewhere. Since the time of Senn, Lemmermann (1907–1910), Pascher (1913c), Skuja (1948) and Huber-Pestalozzi (1950) have given systematic treatments of various genera comprising the complex, and Drouet and Cohen (1935, 1937) have given a good account of the morphology of *Gonyostomum semen.* Fritsch (*in* West, 1927, p. 405) elevated the group to the rank of class.

The majority of authors have regarded the Chloromonadophyceae as an isolated group of flagellates of uncertain relationship (cf. Fritsch, 1935, p. 723; Smith, 1950, p. 625). Prescott (1951, p. 421) has in fact erected a phylum Chloromonadophyta for the group. Oltmanns (1922a, p. 44) recognized the correspondence between the chloromonads on the one hand and the euglenids and the cryptomonads on the other, but made it clear that he like many others was not sure that this implied a definite relationship.

Both Skuja (1948) and Huber-Pestalozzi (1950, p. 2) place the Chloromonadophyceae, Cryptophyceae, and Dinophyceae as classes in the phylum Pyrrophycophyta. The uniflagellate genus *Monomastix* shows relationships to both the Chloromonadophyceae and the Cryptophyceae. Huber-Pestalozzi (1950, p. 2) considers it the type of a subclass in the Cryptophyceae whereas Skuja (1948, p. 344) places it in the Chloromonadaceae.

Although neither the Chloromonadophyceae nor the Cryptophyceae appear to be closely related to the Dinophyceae (see the section on the Cryptophyceae regarding Pringsheim's [1944] and Graham's [1951] doubts about the presumed relationship between the Cryptophyceae and Dinophyceae) it is not inconceivable that the Chloromonadophyceae and the Cryptophyceae are at least distantly allied and they are therefore here placed near each other as classes appended to the Pyrrophycophyta. Outstanding points of agreement between these two classes are: (1) the cells are naked and more or less dorsiventral; (2) a longitudinal furrow is present in the cells of both classes; (3) the majority of the forms in both groups are anteriorly biflagellate; (4) trichocysts are present in certain members of both groups; (5) some chloromonads have a cavity at the anterior end of the cell (connected to the exterior by a duct) which is comparable to the "gullet" of some cryptomonads.

A conspicuous but phylogenetically perhaps insignificant difference between the two groups is the storage of reserve food as starch or starchlike compounds in the Cryptophyceae and as oil in the Chloromonadophyceae. The flagella in the two groups are also of a somewhat different structure and are arranged differently.

The systematic arrangement here adopted is essentially that of Huber-Pestalozzi (1950), except that *Monomastix* is considered, in agreement with Skuja (1948), as belonging to the Chloromonadophyceae instead of the Cryptophyceae.

Class CHLOROMONADOPHYCEAE (Klebs) Fritsch orth. mut. Drouet et Cohen (1935, p. 423)

Syn.: Raphidophycinées Chadefaud (1950a, p. 789)

Order MONOMASTIGALES (Huber-Pestalozzi) Papenfuss, stat. nov.

Syn.: Subclass Monomastiginae Huber-Pestalozzi (1950, p. 2)

Family Monomastigaceae Huber-Pestalozzi (1950, p. 2)

Order CHLOROMONADALES Engler (1898, p. 8, as "Reihe")
Syn.: Raphidomonadales Chadefaud (1950a, p. 789)
Family Vacuolariaceae Luther (1899, p. 19)
Syn.: Chloromonadaceae Engler (1898, p. 8, *nomen nudum*) ex Prescott (1951, p. 421); Gonyostomaceae Lemmermann (1907–1910, p. 478); Thaumatomastigaceae Skuja (1939b, p. 99); Thaumatonematidae Poche (1913, p. 155)

Phylum Phaeophycophyta

Characterization: The algae belonging to this phylum owe their characteristic olive-green to dark brown color to the presence in their plastids of certain xanthophylls, especially fucoxanthin (which is peculiar to them and to diatoms), that mask the other pigments: chlorophyll *a*, chlorophyll *c*, and beta-carotene.

Depending upon the genus or species, the cells possess one to many plastids of varying form and size. Pyrenoids have been recorded for a number of species but these structures may not be true pyrenoids. Ordinarily the cells are uninucleate. The cell wall is differentiated into an inner cellulosic and an outer pectic portion consisting usually of a gumlike substance, algin, which has many economic uses. Calcification of the wall occurs in the genus *Padina*. The known food reserves are the polysaccharide laminarin, the alcohol mannitol, and fats.

The simplest Phaeophycophyta, as exemplified by certain members of the order Ectocarpales, have a branched, uniseriate, filamentous, and frequently microscopic thallus. The orders Laminariales and Fucales are comprised of morphologically elaborate forms that in size, degree of external differentiation, and complexity of structure surpass all other algae.

Growth in length of the thallus is apical or marginal as the result of a single initial or a row of initials. Some show diffuse growth. Many possess an intercalary meristem. In the Laminariales it is situated between the stipe and blade and contributes cells to both; in other groups (e. g., Desmarestiales) it is located at the base of a terminal hair. Growth in width, thickness, or girth of the thallus is effected by repeated longitudinal division of the first-formed segments, or by the formation of radially directed filaments. In many forms the surface layer of cells remains meristematic and through periclinal division contributes to the growth in girth or thickness.

The majority of brown algae show an alternation of generations. The two generations may be morphologically identical (isomorphic) or dissimilar (heteromorphic). The diploid asexual generation forms either unilocular sporangia, plurilocular sporangia, or both. The unilocular sporangium develops from a single cell, which is not partitioned by walls. It is the seat of meiosis. The haploid zoöspores (aplanospores in the Dictyotales) that are produced in it give rise to sexual plants. The plurilocular sporangia are formed by a linear series of cells (or rarely a single cell) that are divided into compartments, in each of which is formed a single zoöspore. No reduction of chromosome number occurs in these sporangia. Their zooids give rise to other diploid, sporophytic plants.

The sexual plants are monoecious or dioecious and they are either isogamous, anisogamous, or oögamous. In isogamous and anisogamous forms the gametangia are plurilocular organs that in structure agree with the plurilocular sporangia of the sporophytic generation. In oögamous species one or more eggs are produced in each oögonium and one or many sperms in each antheridium.

The motile reproductive cells are pear-shaped, usually possess an eye-spot, and are laterally biflagellate.[9] The anteriorly directed flagellum is longer than the posteriorly directed one, except in the Fucales, whose sperms have a long posterior and a short anterior flagellum. Longest (1946) has shown that in *Ectocarpus* the long anterior flagellum is of the tinsel type, an observation that has been confirmed by Manton and

9. This is true even of the sperms of *Dictyota*, which were described by Williams (1904b) as possessing only an anterior flagellum. Shortly afterwards, however, he discovered the presence also of a short posterior flagellum, a fact recently mentioned in his obituary notice by Knight (1947). In a paper that appeared after the manuscript of this chapter had gone to press, Manton, Clarke, and Greenwood (1953), on the contrary describe and illustrate the sperms as being uniflagellate.

Clarke (1951a) with respect to *Pylaiella* and *Laminaria*. It is of interest to note that in the sperms of *Fucus* it is also the anterior flagellum that is of the tinsel type (Manton and Clarke, 1951b).

History: For some fifty years after the publication of Linnaeus' *Species plantarum* (1753) almost all nonmembranous parenchymatous or pseudoparenchymatous algae (brown, red, and green forms such as *Caulerpa*) were referred to the genus *Fucus*. (For the long pre-Linnean history of this genus the reader is referred to the interesting article by Church, 1919a.) Stackhouse in his *Nereis britannica* (1795–1801) and later in his *Tentamen marino-cryptogamicum* (1809) was the first to recognize the heterogeneity of this genus which he accordingly subdivided into a large number of genera, a few of which (*Chorda, Ascophyllum, Bifurcaria*) are still accepted as genera of brown algae.

Largely on the basis of their brown color, Lamouroux (1813) erected a group ("ordre"), Fucacées, for some of the genera of this phylum. He, however, excluded from the Fucacées the members of the Dictyotaceae, which he regarded as representative of a separate "ordre," Dictyotées.

C. Agardh (1817) changed Lamouroux' designation to Fucoideae and considered these algae as constituting one of the five sections into which he divided the algae. Like Lamouroux, C. Agardh failed to make a sharp separation of the algae on the basis of color. In 1817, he placed the Dictyotées of Lamouroux in his section Ulvoideae. In 1824 he removed them to the Fucoideae but he still kept the filamentous brown algae in the Confervoideae.

With few exceptions, the autonomy of the brown algae was henceforth accepted as an established fact. On account of their brown pigment, Harvey (1836) named them Melanospermeae, which designation was changed to Melanophyceae by Ruprecht (1851). Thuret (1850) created the name Phaeosporeae for one of the major taxa into which he (1855) divided the group. De Bary (1881) coined the designation Phaeophyceae, which is now generally accepted as the class name of the group.

The discoveries relating to sexuality and of alternation of generations in the Phaeophyceae contributed immensely to an understanding of the life histories of thallophytes. The two kinds of reproductive organs characteristic of a large majority of these algae were named oösporangia and trichosporangia by Thuret in 1850 (pp. 235, 236), but shortly afterwards (1855, p. 15) he proposed the subsequently employed terms unilocular and plurilocular sporangia. Thuret found that the swarmers from the two kinds of sporangia were morphologically similar, except for size, and remarked (1850, p. 236), "J'ai vu d'ailleurs germer les uns et les autres, ce qui prouve suffisamment leur complète identité."

Studying *Fucus,* Thuret in 1853 observed for the first time in brown algae that only eggs to which sperms had had access would germinate. His classical illustrations of the reproductive organs were published in 1854. Strasburger in 1897 saw the fusion of the egg and sperm nuclei and established that the plants are diploid. His cytological observations were confirmed by Farmer and Williams (1896, 1898) and by Yamanouchi (1909a), who also established that meiosis occurs during the first two divisions of the primary nucleus of the oögonium and antheridium. *Fucus* (and this is true of related genera also) thus was shown to have a life history analogous to that of animals.

The next brown alga in which a conjugation of gametes was observed is

Zanardinia. Reinke (1877, 1878) found that in this genus the swarmers from the plurilocular organs (of which there are two kinds—some with large and some with small locules—both borne on the same plant) are gametes which conjugate in pairs, the smaller zooids functioning as male gametes. This was the first observation of the actual fusion of gametes in brown algae. Reinke noted that in *Zanardinia* the unilocular sporangia occurred on separate plants and found that the swarmers from these sporangia always germinated directly. In view of the occurrence of an alternation of generations in higher cryptogams (as had become well established by this time through the pioneering studies of Hofmeister and others), Reinke had no hesitation in interpreting his observations as indicating the occurrence in *Zanardinia* of a similar alternation between gametophytic and sporophytic generations.

This, then, is the first brown alga which was considered as showing this phenomenon. At first botanists hesitated to accept Reinke's interpretation but its accuracy was established cytologically by Yamanouchi (1911, 1913).

Reinke (1878) and Falkenberg (1879) also observed the fusion of the zooids from the plurilocular organs of *Cutleria,* a genus closely related to *Zanardinia.* Both of them were of the opinion that another alga known as *Aglaozonia* (which bears only unilocular organs) represented the sporophytic generation of *Cutleria.* The evidence in favor of this view accumulated in the course of the next few decades and finally Yamanouchi (1909b, 1912) furnished cytological proof of it.

Berthold (1881b) studying the classical *Ectocarpus siliculosus* at Naples found that also in this genus the zooids from the plurilocular organs were gametes. He also saw the fusion of the gamete nuclei, an observation which had been made only once before in plants—by Schmitz (1879c) in *Spirogyra.* Berthold was unable to determine the role of the unilocular sporangia of *Ectocarpus* since none of the plants obtained in the sea at Naples bore any.

In consequence of the observations of Reinke, Falkenberg, and Berthold regarding the gametic role of the zooids from the plurilocular organs of *Zanardinia, Cutleria,* and *Ectocarpus* a firm conviction developed among botanists (and was adhered to for almost half a century) that the plurilocular organs of brown algae were always gametangia and the unilocular organs sporangia. Not infrequently it was found (e.g., by Berthold, 1881b; Sauvageau, 1896a, 1896b, 1897; Oltmanns, 1899; Kuckuck, 1891) that the zooids from the plurilocular organs did not conjugate but germinated directly. To explain this asexual behavior the theory was usually advanced that the gametes had lost their sexual power and germinated parthenogenetically.

That this explanation was incorrect was shown by Knight (1923, 1929). Studying *Pylaiella* (a genus related to *Ectocarpus*) and *Ectocarpus,* she demonstrated that brown algae had two kinds of plurilocular organs: some occurring on haploid plants and functioning as gametangia and some on diploid plants and functioning as zoösporangia. The diploid plants frequently also formed unilocular sporangia. Meiosis occurred in the unilocular sporangia, as had previously also been shown by Yamanouchi with reference to *Zanardinia* and *Cutleria* and by Kylin (1918) with reference to *Chorda.* No reduction divisions occurred in the plurilocular sporangia of diploid plants and the zooids produced in them germinated directly.

Knight (1923) showed that the life history of *Pylaiella* included an alternation of isomorphic generations. She (1929) was unable, however, to demonstrate an alternation of generations in *Ectocarpus*. Contrary to the long-held view that the zooids from the unilocular organ were zoöspores, she claimed that at least in British waters the zooids from the unilocular organs of *Ectocarpus* functioned as gametes. In this region there thus existed only diploid plants. She repeated the observations of Berthold and others at Naples and found that in that area the plants were haploid and their plurilocular organs were gametangia.

Papenfuss (1933, 1935), working at Woods Hole, Massachusetts, confirmed the observations of Knight that *Ectocarpus* included haploid plants which bear only plurilocular organs and diploid plants which form both unilocular and plurilocular organs. He was unable, however, to confirm her observations regarding the gametic nature of the zooids from the unilocular organs. Instead, he found that *Ectocarpus* exhibited a regular alternation of isomorphic generations. The observations of Papenfuss were confirmed by Føyn (1934) working in Norway.

Several other investigators have claimed a gametic role for the zooids from the unilocular organs of diverse brown algae. Although such behavior is theoretically possible, the evidence presented for the alleged instances of conjugation between these swarmers is not convincing. It would indeed be remarkable if an organism, such as *Ectocarpus siliculosus,* could form gametes on the diploid as well as the haploid generation.

In 1904 Williams demonstrated the occurrence of an alternation of isomorphic generations in *Dictyota* and in 1915 Sauvageau made the epoch-making discovery that *Saccorhiza bulbosa,* a member of the Laminariaceae, possesses an alternation of heteromorphic generations comparable to that of ferns. The familiar macroscopic plant was found to be the sporophyte. The zoöspores formed in its unilocular sporangia give rise to microscopic, filamentous gametophytes which are dioecious and produce oögonia and antheridia.

This very significant discovery of Sauvageau, which was made on the basis of cultures, created a great deal of interest in the brown algae. It was evident that the complete cycle of development of many of these algae could not be ascertained unless they were grown in culture. It was also clear that rich rewards were in store for those who would follow his approach to problems relating to the life histories of brown algae. He himself retained leadership in this fruitful field until his death in 1936. (For a list of his many publications see Dangeard, 1937.)

The knowledge that has accumulated during the past fifty years has naturally had far-reaching effects on the classification of the Phaeophycophyta.

Although Lamouroux (1813), C. Agardh (1817, 1824), and Harvey (1836) had recognized the autonomy of the brown algae, each of them had included in the group certain dark-colored red algae or had assigned representatives of the group to other major taxa.

In 1848 J. Agardh published the first volume of his *Species genera et ordines algarum,* a volume devoted exclusively to the brown algae. The Phaeophycophyta were segregated by J. Agardh into seven tribes (also referred to by him in different places as families or orders), six of which were first recognized by Greville (1830) and Harvey (1836). It is noteworthy that each of these seven groups was later elevated to the rank of order (with altered circumscription, of course).

Between 1848 and 1917, these algae were divided by different authors into two, three, or four major taxa. Thuret (1855, pp. 5–15) recognized four groups: Phaeosporeae, Tilopterideae, Dictyoteae, and Fucaceae. Hauck (1883) recognized three orders: Fucoideae (with one family), Dictyotaceae (with one family), and Phaeozoosporeae (with ten families). Hauck's three groups were retained by De Toni (1895) except that he used, respectively, the names of Cyclosporinae (a designation proposed by Areschoug, 1847, for the Fucaceae), Tetrasporinae, and Phaeozoosporinae.

Kjellman (1891–1893) divided the Phaeophyceae into the two groups Phaeosporeae and Cyclosporeae (with the single family Fucaceae) and removed the Dictyotaceae to an independent group Dictyotales, which he considered as so different from other brown algae that they could not be properly placed with them (see also Falkenberg, 1882, pp. 169, 230–234). (Because they commonly form four immobile spores in their unilocular sporangia, which thus resemble the tetrasporangia of red algae, the Dictyotales were a stumbling block to many students of the algae of the last century.) The Phaeosporeae were divided by Kjellman into the two subgroups Zoogonicae and Acinetae (which included only the Tilopteridaceae). It is apparent that as far as the major categories are concerned Kjellman's system differed but little from that of Thuret.

Oltmanns (1904) segregated the Phaeophyceae into the three groups Phaeosporeae, Akinetosporeae (a designation proposed by Bornet, 1891, p. 370), and Cyclosporeae. The Akinetosporeae received only the Tilopteridaceae (characterized by their immobile monosporangia), but in contrast to earlier systems, Oltmanns placed the oögamous Dictyotaceae as a second family with the likewise oögamous Cyclosporeae (Fucaceae).

In 1917 Kylin revised the classification of the Phaeophyceae, basing his system largely on developmental and nuclear cycles. He recognized five orders: Phaeosporeae, Tilopteridales, Dictyotales, Laminariales, and Fucales. The essentially new feature here is the establishment of the order Laminariales for those Phaeosporeae of earlier systems that had been found to possess an alternation of heteromorphic generations.

During the next ten years the old order Phaeosporeae was further subdivided into the following seven orders: (1) Ectocarpales (Setchell and Gardner, 1922, Oltmanns, 1922b; see Papenfuss, 1947, p. 398, fn., regarding the dates of the works by Setchell and Gardner, and Oltmanns); (2) Sphacelariales (Oltmanns, 1922b); (3) Cutleriales (Oltmanns, 1922b); (4) Chordariales (Setchell and Gardner, 1925); (5) Sporochnales (Sauvageau, 1926); (6) Desmarestiales (Setchell and Gardner, 1925); (7) Dictyosiphonales (Setchell and Gardner, 1925).

Utilizing the recently acquired knowledge of the structure and reproduction of the Phaeophycophyta, Kylin in 1933 erected a new system of classification of these algae. He divided them into three classes and a total of twelve orders, one of which (the Punctariales) he established in this paper as a segregate from the Ectocarpales. The first class, the Isogeneratae, received forms that showed an alternation of isomorphic generations. It included the orders Ectocarpales, Sphacelariales, Cutleriales, Tilopteridales, and Dictyotales. The second class, the Heterogeneratae, comprised forms which showed an alternation of heteromorphic generations. It included two subclasses, the Haplostichineae and the Polystichineae. In the Haplostichineae no intercalary longitudinal divisions occur in the thallus and consequently no true parenchymatous tissues are formed. In the Polystichineae intercalary longitudinal divisions are formed and hence true parenchymatous tissues are produced. The Haplostichineae received the orders Chordariales, Sporochnales, and Desmarestiales, whereas the Polystichineae received the Punctariales, Dictyosiphonales, and Laminariales. The third class, the Cyclosporeae, received the single order Fucales.

The separation of the Ectocarpales *sensu* Oltmanns (1922b) into haplostichous and polystichous groups was first proposed by Kuckuck (*in* Oltmanns, 1922b; 1929). It is to be noted, however, that Kylin employed this character only with reference to the Heterogeneratae. Papenfuss (1947) has merged the Punctariales in the Dictyosiphonales. It would seem that Kylin (1947) also arrived at the conclusion that these two orders are synonymous, since in the body of his paper he placed *Dictyosiphon* in the Punctariales even though in the introduction (p. 4) he accepted both orders. Arasaki (1949) argues in favor of retention of both orders but the evidence produced is hardly sufficient.

The system of Kylin has received wide recognition. Among those who have not accepted it or have accepted it only in part are Hygen, Fritsch, and more recently Papenfuss. Hygen (1934) is dissatisfied with Kylin's arrangement largely because the Isogeneratae includes a heterogeneous assortment of algae that could not be regarded as forming a phylogenetically coherent unit.

Fritsch (1943, 1944, 1945) does not accept the orders Chordariales, Punctariales, and Dictyosiphonales but retains the families comprising them in the Ectocarpales largely because he believes (1944, p. 254) that their heteromorphic life cycle is derived "by divergent development of the two generations, from an isomorphic alternation, comparable to that exhibited by the Ectocarpaceae." It seems very likely, however, that the other groups with a heteromorphic alternation of generations (the oögamous Sporochnales, Desmarestiales, and Laminariales) also evolved, even if not directly, from the Ectocarpales. The Ectocarpales *sensu* Fritsch includes a very heterogeneous assemblage of algae.

Papenfuss (1951b) accepts all the orders recognized by Kylin, except the Punctariales, but rejects the classes Isogeneratae, Heterogeneratae, and Cyclosporeae and the subclasses Haplostichineae and Polystichineae of the Heterogeneratae. Such an arrangement allows for the parallel and independent evolution of groups with an alternation of isomorphic or heteromorphic generations; it recognizes the Ectocarpales as the possible ancestral stock from which had emerged several orders; and it takes cognizance of the fact that the Fucales are parenchymatous (polystichous) and that parenchymatous forms also occur in the Isogeneratae (e.g., Dictyotales, Sphacelariales). In agreement with Kylin (1933, 1937c, 1938, 1940b) and Fritsch (1945, pp. 380–381), Papenfuss regards the Fucales as occupying an isolated position in the Phaeophyceae.

Recently Feldmann (1949) established an order Scytosiphonales for certain Dictyosiphonales, but the more significant distinguishing features of the new order are based on the acceptance of observations of extremely questionable accuracy.

On the basis of pigment composition, the Phaeophycophyta appear to be related, even if only remotely, to both the Chrysophycophyta, especially the Bacillariophyceae, and the Pyrrophycophyta (cf. Strain, 1951, p. 253). The evidence derived from the structure of the flagella in these three groups (Petersen, 1918, 1929; Vlk, 1931, 1938; Deflandre, 1934; Longest, 1946; Koch, 1951; Manton and Clarke, 1951a, 1951b) suggests that a closer relationship exists between the Phaeophycophyta and Chrysophycophyta than between either of these two groups and the Pyrrophycophyta.

The following arrangement of the Phaeophycophyta is essentially that of Papenfuss (1951a).

Phylum PHAEOPHYCOPHYTA Papenfuss (1946, p. 218)
Syn.: Phaeophyta Wettstein (1901, p. 46)
Class PHAEOPHYCEAE De Bary (1881, p. 14)
Syn.: Melanospermeae Harvey (1836, p. 157); Melanophyceae Ruprecht (1851, p. 206); Phycophéinophycées Marchand (1895, p. 15)
Order ECTOCARPALES Setchell et Gardner (1922, p. 403)
Family Ectocarpaceae (C. Agardh) Kützing orth. mut. Harvey (1849, p. 11)
Syn.: Streblonemaceae Kylin (1947, p. 45), *nomen nudum;* Acinetosporaceae Bornet orth. mut. Hamel (1931, p. 8; cf. Kornmann, 1953)
Family Ralfsiaceae Hauck (1883, p. 318)
Syn.: Lithodermataceae Hauck (1883, p. 318); Strangulariaceae Strömfelt (1886, p. 49); Nemodermataceae Feldmann (1937, p. 121)
Order SPHACELARIALES Oltmanns (1922b, p. 83)
Syn.: Discosporangiales O. C. Schmidt (1937a, p. 3)
Family Sphacelariaceae J. Agardh orth. mut. Cohn (1872a, p. 17)
Family Stypocaulaceae Oltmanns (1922b, p. 95)
Family Cladostephaceae Oltmanns (1922b, p. 102)
Family Choristocarpaceae Kjellman (1891, p. 190)
Syn.: Discosporangiaceae O. C. Schmidt (1937a, p. 3)
Order CUTLERIALES Oltmanns (1922b, p. 109)
Family Cutleriaceae (Thuret) Hauck (1883, p. 318)
Order TILOPTERIDALES Kylin (1917, p. 308)
Family Tilopteridaceae (Thuret) Cohn orth. mut. De Toni (1891b, p. 182)
?Family Masonophycaceae O. C. Schmidt (1937b, p. 5)
Order DICTYOTALES Kjellman (1893, p. 291)
Family Dictyotaceae Lamouroux orth. mut. Dumortier (1829, p. 76)
Syn.: Zonariaceae (S. F. Gray) Nägeli (1847, p. 179)
Order CHORDARIALES Setchell et Gardner (1925, p. 570)
Family Myrionemataceae (Nägeli) Foslie orth. mut. Skottsberg (1907, p. 49)
Family Elachistaceae Kjellman (1890, p. 41)
Family Corynophlaeaceae Oltmanns (1922b, p. 23)
Syn.: Leathesiaceae Setchell et Gardner (1925, p. 507)
Family Chordariaceae (C. Agardh) Greville orth. mut. Harvey (1849, p. 11)
Syn.: Mesogloeaceae Kützing (1843, p. 32); Myriogloiaceae Kuckuck ex Setchell et Gardner (1925, p. 555); Heterochordariaceae Setchell et Gardner (1925, p. 549); Aegiraceae Setchell et Gardner (1925, p. 543); Myriocladiaceae Kuckuck (1929, p. 63)
Family Spermatochnaceae Kjellman (1890, p. 32)
Syn.: Stilophoraceae (Nägeli) De Toni et Levi orth. mut. Kjellman (1890, p. 34)
Family Acrothrichaceae (Oltmanns) Kuckuck (1929, p. 66)
Family Chordariopsidaceae Kylin (1940a, p. 53)
Family Splachnidiaceae Mitchell et Whitting (1892, p. 9)

Order SPOROCHNALES Sauvageau (1926, p. 364)
Family Sporochnaceae Greville orth. mut. Harvey (1849, p. 10)
Order DESMARESTIALES Setchell et Gardner (1925, p. 554)
Syn.: Arthrocladiales Sauvageau (1931, p. 117)
Family Arthrocladiaceae Chauvin orth. mut. Hauck (1883, p. 317)
Family Desmarestiaceae (Thuret) Kjellman (1880, p. 10)
Order DICTYOSIPHONALES Setchell et Gardner (1925, p. 586)
Syn.: Punctariales Kylin (1933, p. 93); Scytosiphonales Feldmann (1949, p. 112)
Family Striariaceae Kjellman (1890, p. 53)
Syn.: Stictyosiphonaceae (Kjellman) Kuckuck (1929, p. 80)
Family Giraudyaceae (Kjellman) Hygen (1934, p. 210)
Family Myriotrichiaceae Kjellman (1890, p. 46)
Family Punctariaceae (Thuret) Kjellman (1880, p. 9)
Syn.: Encoeliaceae (Bory) Kützing orth. mut. Kjellman (1890, p. 55); Asperococcaceae (Zanardini) De Toni et Levi orth. mut. Foslie (1890, p. 88); Litosiphonaceae Kuckuck (1929, p. 80), *nomen nudum;* Sorantheraceae Kuckuck (1929, p. 80), *nomen nudum*
Family Scytosiphonaceae (Thuret) Hauck (1883, p. 317)
Syn.: Phaeosaccionaceae Feldmann (1949, p. 112)
Family Chnoosporaceae Setchell et Gardner (1925, p. 552)
Family Dictyosiphonaceae Kützing orth. mut. Kjellman (1890, p. 49)
Syn.: Coilodesmaceae (Kjellman) Setchell et Gardner (1925, p. 577)
Order LAMINARIALES Kylin (1917, p. 308)
Family Chordaceae Dumortier (1822, pp. 72, 102)
Family Laminariaceae (C. Agardh) Dumortier orth. mut. Dumortier (1829, p. 77)
Syn.: Phyllariaceae (Kjellman) Hamel (1938, p. 304)
Family Lessoniaceae (Setchell) Setchell et Gardner (1925, p. 621)
Family Alariaceae (Kjellman) Setchell et Gardner (1925, p. 633)
?Family Prototaxitaceae Pia (1927, p. 95)
Order FUCALES Kylin (1917, p. 309)
Family Ascoseiraceae Skottsberg (1907, p. 148)
Family Durvilleaceae (Oltmanns) De Toni (1891b, p. 173)
Family Notheiaceae Kuckuck (1929, p. 12) ex O. C. Schmidt (1938, p. 224)
Syn.: Hormosiraceae (Gruber) Fritsch (1944, p. 257)
Family Fucaceae Lamoroux orth. mut. Dumortier (1822, p. 72)
Family Himanthaliaceae (Kjellman) De Toni (1891b, p. 173)
Family Cystoseiraceae Kützing orth. mut. De Toni (1891b, p. 173)
Family Sargassaceae (Decaisne) Kützing orth. mut. De Toni (1891b, p. 174)

PHYLUM SCHIZOPHYTA

CLASS SCHIZOPHYCEAE

Characterization: As a class the Schizophyceae (Cyanophyceae, Myxophyceae) or bluegreen algae as they are commonly called are sharply distinguished from the other large groups of algae. The low state of cell differentiation, the bluegreen color of the thalli, the production of cyanophycean starch (Kylin, 1943a) and the absence of an organized nucleus are characters that clearly set them apart. There is at present no good evidence indicating that they evolved from flagellated ancestors or that they are the direct ancestors of other algal groups, although a very distant relationship with the red algae is not improbable.

The simplest Schizophyceae are unicellular. In many instances, however, the individual cells remain attached to one another to form colonies of various shapes and sizes. The more advanced types are filamentous. The filaments are simple or branched and may be aggregated. The branched forms exhibit false or true branching or both types of branching. The individual cells of the unicellular forms and the filaments of the filamentous species are usually enveloped by a gelatinous sheath that may be homogeneous or stratified and frequently is pigmented. The inner portion of the sheath contains a small amount of cellulose (Kylin, 1943a).

In the majority of bluegreen algae, two regions are distinguishable within the protoplast: a peripheral region, the chromoplasm, which contains the pigments, and a colorless central region, the central body or centroplasm. Ordinarily the protoplast contains no evident vacuoles.

Recent work indicates that the pigments in the chromoplasm occur in small bodies (Calvin and Lynch, 1952). The pigments consist as far as known of chlorophyll *a*, beta-carotene and another carotene (flavacin) found only in Schizophyceae, two xanthophylls that are peculiar to these algae, and two proteinaceous pigments (phycobilins), the blue *c*-phycocyanin and the red *c*-phycoerythrin (Strain, 1951, p. 253).

The centroplasm contains various kinds of bodies, including some that are in the form of granules, rods, or reticula and become evident after application of the Feulgen nuclear reaction. The bodies are not bounded by a nuclear membrane, however, and no nucleoli appear to be present.

In the Stigonemataceae and certain Scytonemataceae adjoining cells are united by pit connections. Only one such connection is present between any two cells and it is always a primary pit connection.

All of the filamentous bluegreen algae, with the exception of the Oscillatoriaceae, regularly form a special type of cell known as a heterocyst. They originate from vegetative cells and have a thickened wall. Intercalary heterocysts have a conspicuous pore at each end; terminal heterocysts have a pore only at the proximal end. The filaments frequently break at the heterocysts and these structures indirectly function in vegetative multiplication. In some instances they have been observed to produce new filaments. (See Fritsch, 1951, for a discussion on these cells.)

As far as known sexual reproduction does not occur in the Schizophyceae. Vegetative multiplication by fission in the unicellular or colonial forms is of common occurrence. In the order Hormogonales the chief method of multiplication is by short lengths of the vegetative filaments called hormogonia. The hormogonia are delimited by the death of occasional cells at intervals along the length of the filament. In certain forms the hormogonia are modified as organs of perrenation (hormocysts).

Many of the filamentous genera, but no Oscillatoriaceae, form thick-walled resting spores known as akinetes. In certain genera of the Chamaesiphonales the contents of a cell divide into a number of endospores. These spores are thin-walled and germinate directly to produce new plants.

The bluegreen algae live in many kinds of habitats. Many are aquatic in freshwater or marine situations; others are terrestrial or subaerial in occurrence. A number of forms grow in hot springs, at times with a temperature as high as 85° C. Many forms live in association with other organisms—plants and animals. Species belonging principally to the genera *Gloeocapsa*, *Nostoc*, *Scytonema*, and *Stigonema* constitute the algal associate in many lichens. A number of species are able to fix atmospheric nitrogen.

History: Although members of this class have been known to the world of science since the time of Linnaeus (1753), who described a few species under the generic names *Tremella, Byssus,* and *Ulva,* the distinctive features of the class remained unrecognized until the middle of the nineteenth century. To be true C. Agardh in 1824 established an order Nostochinae (one of six into which he divided the algae) to receive *Nostoc* and *Rivularia,* but he also assigned to this order several genera belonging to unrelated groups of algae and referred other genera of bluegreen algae (e.g., *Oscillatoria*) to the order Confervoideae.

The bluegreen algae were first recognized as constituting an autonomous group (order) of algae by Stizenberger in 1860 (p. 18). He called them Myxophyceae, adopting a designation (Myxophykea) previously used by Wallroth (1833, p. ix) for a heterogeneous assemblage of algae, including representatives of the Schizophyceae. Stizenberger remarked that these algae were distinguishable from other algal orders by their pigments.

Rabenhorst (1863, p. 1) established a division for these algae which, on the basis of color, he named Phycochromaceae. As one of the features of the group, Rabenhorst mentioned the absence of a nucleus in the cells, a character previously remarked upon by Nägeli (1849, p. 45) with reference to some of the unicellular members of the assemblage.

Rabenhorst credited the group with six families, viz., Chroococcaceae, Oscilla[to]riaceae, Nostocaceae, Rivulariaceae, Scytonema[ta]ceae, and Sirosiphonaceae (= Stigonemataceae), all of which are still accepted, although usually with modified circumscriptions.

In 1865 Rabenhorst regarded the bluegreen algae as a class and changed the divisional name Phycochromaceae, which he had given them in 1863, to Phycochromophyceae. At this time Rabenhorst divided the class into two orders: "Ordo I. Cystiphorae," in which he placed the family Chroococcaceae, comprised of unicellular and colonial forms, and "Ordo II. Nematogenae," to which he referred the remaining five families of his treatment of 1863, all of which included filamentous forms.

On account of their blue pigment, Sachs (1874) named these algae Cyanophyceae. Because of the appropriateness of this designation and because of the fame of Sachs and his textbook, the name Cyanophyceae immediately gained favor among botanists, and it is still used by many.

Cohn (1880, p. 286) gave these algae the name Schizophyceae.[10] He regarded them as a group coordinate with the bacteria (which he in 1872[a] had named Schizomycetae) and placed both groups in his order Schizosporeae, as he had first done in 1872 (a and b). That there existed a relationship between these two groups of organisms had already been pointed out by Cohn as early as 1854.

Engler (1892) divided the thallophytes into two divisions, the Myxothallophyta and the Euthallophyta. Under the latter he had a number of subdivisions, one of which was Schizophyta, to which he referred the two classes Schizophyceae and Schizomycetes. Without giving the reference, Pringsheim (1949, p. 48) and others credit Cohn with the name Schizophyta, but I have been unable to find this designation in Cohn's publications. It apparently was used for the first time by Falkenberg (1882, p. 162) as the name of an order comprising both the bluegreen algae and the bacteria.

In conformity with the views of Cohn and the system of Engler, which has had many adherents down to the present, the bluegreen algae are here regarded as constituting a class, the Schizophyceae, coordinate with the bacteria (class Schizomyceteae) in the phylum Schizophyta. It should be pointed out, however, that many biologists do not believe that these two (or several) groups of organisms are related. This latter view has been particularly well defended by Pringsheim (1949), to whom the reader is referred for a detailed discussion of the question (see also Stanier and van Niel, 1941).

Although the characters which point to an affinity between bacteria and

10. It is to be noted, however, that Rabenhorst (1847, pp. V, 16) had previously used the designation Schizophyceae for a "suborder" of algae comprising the diatoms and desmids.

bluegreen algae are largely of a negative kind, as Pringsheim has emphasized, there is little reason for believing that certain negative characters are less important than positive characters as indicators of phylogenetic relationship. Furthermore, if present-day bacteria and bluegreen algae had evolved from common ancestors affinities should be sought primarily among the simpler members of both groups (the Eubacteriales and the Chroococcales, respectively), since they are the forms which may be expected to have retained and consequently show the largest number of ancestral characters. The morphological similarity between certain members of the Eubacteriales and members of the Chroococcales suggests that a relationship does exist between these two groups. Further evolution in the bluegreen algae has resulted in the development of thalli which are much more elaborate than those of the higher bacteria. But morphological differences of comparable magnitude are not uncommon among groups of organisms which are known to be phylogenetically related and their occurrence in the Schizophyta do not necessarily speak against a common origin of bacteria and bluegreen algae.

On the basis of method of multiplication, Thuret as long ago as 1875 subdivided the bluegreen algae, or Nostochinées as he called them, into two tribes: (1) the Chroococcaceae or Coccogoneae, which show vegetative propagation by single cells, and (2) the Nostochineae or Hormogoneae, which reproduce vegetatively by short rows of cells (hormogonia). Thuret segregated the Hormogoneae into two subtribes: (1) Psilonemeae, in which the filaments lack hairlike tips, and (2) Trichophoreae, in which the filaments possess hairlike apices. In Thuret's time the members of the subsequently established family Chamaesiphonaceae were only poorly known.

To Nägeli (1849) and Hansgirg (1888b, 1892) we are indebted for much of the fundamental information on which present-day classification of the Chroococcaceae rests. Current classification of Thuret's Hormogoneae is largely based on the systems of Borzi (1878, 1879, 1882), Bornet and Flahault (1886–1888), and Gomont (1892, 1893).

The first comprehensive treatment of the Schizophyceae as a whole was given by Kirchner (1898), who followed, as far as the broad outlines are concerned, the classification of Rabenhorst (1865), Thuret (1875), and Hansgirg (1888b, 1892). In accordance with the system of Thuret, Kirchner divided the bluegreen algae into Coccogoneae and Hormogoneae. In the Coccogoneae he placed the Chroococcaceae and the Chamaesiphonaceae, a family established by Borzi in 1882. The Hormogoneae were segregated, in agreement with Thuret, into the Psilonemateae (which received the families, Oscillatoriaceae, Nostocaceae, Scytonemataceae, and Stigonemataceae) and the Trichophoreae (in which were placed the Rivulariaceae and the Camptotrichaceae). As has been pointed out by Fritsch (1944, p. 262), this division of the Hormogoneae (= Hormogonales) by Thuret and Kirchner into two groups on the absence or presence of hairs at the tips of the filaments overemphasized the systematic value of a minor character, and is no longer adhered to.

Adopting and amending a classification introduced by Stizenberger (1860), Bornet and Flahault (1886, p. 325) and Gomont (1892) divided the Hormogoneae into the two groups Heterocysteae and Homocysteae according as the trichomes contain or lack heterocysts. Kirchner (1898, p. 49) and Fritsch (1944) have emphasized, however, that related genera are segregated by this division. In more recent times the division of the Hormogonales into Heterocysteae and Homocysteae has been followed by Setchell and Gardner (1919) and by Smith (1933) who, however, has since abandoned this classification (Smith, 1950).

In 1895 Marchand established the ordinal names Coccogonées and Hormogonées (changed to Coccogonales and Hormogonales by Atkinson, 1905, p. 163) for the two tribes of Thuret. The name Hormogonales is still accepted by many phycologists but the designation Coccogonales has been abandoned in favor of Chroococcales, which was proposed by Wettstein (1924).

Borzi had already in 1878 divided the order Nematogenae of Rabenhorst into the two suborders Hormogoneae and Cystogoneae. The latter suborder included only his new family Chamaesiphonaceae (p. 238) whereas the former received the Nostocaceae, Scytonemataceae, Rivulariaceae, and Oscillatoriaceae. Borzi placed, as others before him had done, the Chroococcaceae in an order by itself, which he called Gloeogenae. Following up the train of thought of Borzi, Hansgirg (1892, p. 17) divided the bluegreen algae into the three orders Gloeosipheae (= Hormogonales), Chamaesiphonaceae, and Chroococcoideae. The order Chamaesiphonaceae received attached, unicellular (*Chamaesiphon*) or filamentous (*Clastidium*) forms, which occur as solitary individuals or as colonies, lack hormogonia and heterocysts, and multiply by spores (endospores) produced in basipital succession.

Finally in 1924 Wettstein proposed the currently accepted designation Chamaesiphonales for the family Chamaesiphonaceae.

In his treatment of the Schizophyceae in De Toni's *Sylloge algarum,* Forti (1907) followed the classification of Kirchner. Borzi, shortly afterward in a series of papers (1914, 1916, 1917), presented a revision of his earlier (1878, 1879, 1882) classification of these algae. Some of the new features of this system were later adopted by Geitler in the development of his system.

By the year 1925, the Schizophyceae had thus by degrees come to be segregated into three orders and a total of 14 families, including one (Microchaetaceae) which had been erected by Lemmermann in 1907, two (Hyellaceae and Borziaceae) which were established by Borzi in 1914, and three (Nodulariaceae, Leptobasaceae and Loefgreniaceae) which were created by Elenkin in 1916 and 1917.

In 1925 (a and b) Geitler published a system which formed a radical departure from previous classifications. He divided the bluegreen algae into seven orders and a total of 19 families. Shortly afterward Geitler (1930–1932) abandoned in part his system of 1925 and recognized only the three old orders Chroococcales, Chamaesiphonales, and Hormogonales. At this time Geitler regarded the Schizophyceae as comprised of 21 families, the majority of which were the same as those accepted in 1925 but some of the ones recognized in 1925 were reduced and several new ones were added. In 1942 (pp. 37 ff.) Geitler returned in part to his system of 1925 and recognized four orders (Chroococcales, Pleurocapsales, Dermocarpales, Hormogonales) and 22 families.

In 1938 and 1949 appeared the first and second fascicles, respectively, of the systematic part of Elenkin's monumental work on the freshwater and terrestrial Schizophyceae of Russia. Elenkin elaborated upon Geitler's systems of 1925 and 1930–1932, and recognized, as far as the groups under consideration by himself were concerned, no fewer than 12 orders and 47 families.

It is to be regretted that both Geitler and Elenkin have burdened the already involved nomenclature of the Schizophyceae with a number of unnecessary names. These authors have violated the Code by renaming families whose circumscription they have changed but which still include the type of the rejected family or, in the case of Geitler, by renaming families if the generic name from which a family name was derived has been reduced to synonymy.

Fritsch (1942, 1944, 1945) accepts in part Geitler's system of 1925 and divides the Schizophyceae into the five orders Chroococcales, Chamaesiphonales, Pleurocapsales, Nostocales and Stigonematales. In the division of the class into five orders, the system of Fritsch corresponds closely to that of Geitler as amended in 1942, except that Geitler at this time maintained the order Hormogonales as a single taxon (as he had also done in 1930–1932) whereas Fritsch recognizes in its place the two orders Nostocales and Stigonematales, as Geitler had in 1925.

Fritsch (1945) arranges the genera in 19 families, all of which, with the exception of the Cyanochloridaceae and Loefgreniaceae, were recognized also by Geitler (1942), although the two authors do not always use the same names or place the families in the same order.

Frémy (1930, 1933), Copeland (1936), Huber-Pestalozzi (1938), Lindstedt (1943), Skuja (1948), Smith (1950), Prescott (1951), and others accept only the three original orders Chroococcales, Chamaesiphonales, and Hormogonales, except that Copeland and Smith use the name Oscillatoriales Copeland (1936) instead of Hormogonales. Drouet (1951), however, recognizes no orders in the bluegreen algae and accepts only eight families.

Evidently little agreement exists among students of the Schizophyceae as regards the classification of the class. This disagreement is attributable not so much to lack of knowledge of the morphology of these algae (although it seems likely that cultural studies will yield information that will be useful in the taxonomy of the group) as it is to the paucity of sharply defined characters and the existence of intermediate types which preclude the establishment of clear-cut taxa. The wide divergence in the systems proposed by the various specialists on the group hinges primarily on the taxonomic value assigned to the available characters. In his recognition of only eight families and the suppression of all orders, Drouet is probably guided by the existence of transitional types, although he has not yet presented the detailed arguments upon which his decisions are based.

The separation of the class into the three orders Chroococcales, Chamaesiphonales, and Hormogonales takes account of the structure of the thalli (unicellular or colonial or pseudofilamentous in the Chroococcales, unicellular or pseudofilamentous or filamentous in the Chamaesiphonales, multicellular and filamentous in the Hormogonales) and the method of multiplication (vegetatively by cell division or colony fragmentation in the Chroococcales, by endospores in the Chamaesiphonales, by hormogonia and in some instances by akinetes in the Hormogonales).

The division of the Chamaesiphonales into the two orders Chamaesiphonales and Pleurocapsales by Fritsch (1942, 1944, 1945) and Geitler (1942, as Dermocarpales and Pleurocapsales) takes cognizance of differences in thallus organization—the Chamaesiphonales receiving plants which are unicellular and with the cells exhibiting polarity as contrasted with the filamentous and frequently heterotrichous habit of the forms placed in the Pleurocapsales. It is to be noted, however, that these two authors do not in all instances agree in their assignment of families to these two orders.

The separation of the Hormogonales into Nostocales and Stigonematales by Fritsch is based on the occurrence of true branching and the heterotrichous habit of the thalli in some forms (Stigonematales) as contrasted with the unbranched or falsely branched condition of the filaments in others (Nostocales).

The division of the bluegreen algae by Elenkin into a large number of orders and families is an attempt to segregate the genera on the basis of small differences into seemingly clear-cut groups. Elenkin (1933) thus, for example, elevates the Chroococcaceae to the rank of order and divides it into ten families on the basis of the planes of division of the cells and the geometric form of the colonies. Subdivision to the extent proposed by Elenkin is probably unwarranted since it removes from one another forms which seemingly are so closely related that some authors (e.g., Drouet and Daily, 1952) reduce them to a bare few genera and species.

The following synoptic arrangement of the orders and families is the author's compromise of the various recent systems of classification of the Schizophyceae[11]. According to the current Code, the nomenclature of the Chroococcales and Chamaesiphonales starts with Linnaeus (1753), that of the Oscillatoriaceae (Hormogonales) with Gomont (1892–1893), and that of all other Hormogonales with Bornet and Flahault (1886–1888).

Phylum SCHIZOPHYTA (Falkenberg) Engler (1892, p. 3)
  Class Schizophyceae Cohn (1880, p. 286)
    Syn.: Division Phycochromaceae Rabenhorst (1863, p. 1); Class Phycochromophyceae Rabenhorst (1865, p. 1): Order Myxophyceae Stizenberger (1860, p. 18); Cyanophyceae Sachs (1874, pp. 248, 251); Phycocyanophycées Marchand (1895, p. 11.) Non Schizophyceae Rabenhorst (1847, pp. v, 16)
    Order CHROOCOCCALES Wettstein (1924, p. 79)
      Syn.: Entophysalidales Geitler (1925a, p. 223); Tubiellales Elenkin (1934, p. 56); Coccogonales (Thuret) Marchand orth. mut. Atkinson (1905, p. 163)
        Family Chroococcaceae Nägeli (1849, p. 40)
          Syn.: Coccobactreaceae Elenkin (1933, p. 19); Beckiaceae Elenkin (1933, p. 19); Merismopediaceae Elenkin (1933, p. 19); Microcystidaceae Elenkin (1933, p. 19); Gloeocapsaceae Elenkin (1933, p. 19); Coelosphaeriaceae Elenkin (1933, p. 19); Gomphosphaeriaceae Elenkin (1933, p. 19); Woronichiniaceae Elenkin (1933, p. 19); Holopediaceae Elenkin (1933, p. 19); Cyanidiaceae Geitler (1933, p. 624)
        Family Entophysalidaceae Geitler (1925a, p. 235)
          Syn.: Chlorogloeaceae Geitler (1925a, p. 235); Tubiellaceae Elenkin (1934, p. 56)
    Order CHAMAESIPHONALES Wettstein (1924, p. 79)
      Syn.: Pleurocapsales Geitler (1925a, p. 238); Dermocarpales Geitler (1925a, p. 238); Siphononematales Geitler (1925a, p. 238); Endonematales Elenkin (1934, p. 57)
        Family Pleurocapsaceae Geitler (1925a, p. 238)
          Syn.: Chroococcidiaceae Geitler (1933, p. 623); Xenococcaceae Ercegović (1932, p. 138); Podocapsaceae Ercegović (1932, p. 138)

11. Several groups of organisms (other than the Beggiatoaceae) which have been placed with the bacteria (Achromatiaceae, Vitreoscillaceae, Thriotrichaceae, Cyanochloridaceae) but which may be bluegreen algae, or at least include forms which probably are bluegreen algae, are discussed by Pringsheim (1949).

Family Hyellaceae Borzi (1914, p. 359)
Syn.: Scopulonemataceae Ercegović (1932, p. 138)
Family Dermocarpaceae Geitler (1925a, p. 247)
Family Clastidiaceae Drouet et Daily (1952, p. 223)
Family Chamaesiphonaceae Borzi (1882, p. 298)
Family Siphononemataceae Geitler (1925a, p. 251)
Family Endonemataceae Pascher (1929b, p. 347)
Syn.: Pascherinemataceae Geitler (1942, p. 99)

Order HORMOGONALES (Thuret) Marchand orth. mut. Atkinson (1905, p. 163)
Syn.: Gloeosiphonales Wettstein (1924, p. 80); Oscillatoriales Copeland (1936, p. 78); Nostocales Geitler (1925a, p. 252); Stigonematales Geitler (1925a, p. 252); Mastigocladales Elenkin (1938, p. 528); Diplonematales Elenkin (1938, p. 535)

Family Oscillatoriaceae (S. F. Gray) Dumortier ex Kirchner (1898, p. 61)
Syn.: Borziaceae Borzi (1914, p. 358); Beggiatoaceae (Hansg.) Migula (1895, p. 41); Pseudonostocaceae Elenkin (1949, p. 1222); Schizothrichaceae Elenkin (1949, p. 1668); Crinaliaceae Elenkin (1949, p. 1845); Vaginariacées (Gomont) Marchand (1895, p. 12); Lyngbyacées Kützing orth. mut. Marchand (1895, p. 12)

Whether the Beggiatoaceae are colorless bluegreen algae or bacteria has been a matter of disagreement for a long time. The evidence in favor of placing them in the Schizophyceae is presented by Pringsheim (1949).

Family Gomontiellaceae Elenkin (1936, p. 543)
Family Nostocaceae Dumortier ex Engler (1892, p. 4)
Syn.: Anabaenaceae Elenkin (1938, p. 643); Aphanizomenonaceae Elenkin (1938, p. 845)
Family Microchaetaceae Lemmermann (1907, p. 101)
Syn.: Nodulariaceae Elenkin (1916, not seen, cited from Geitler, 1942, p. 159); Leptobasaceae Elenkin (1917, p. 164)
Family Rivulariaceae Kützing ex Bornet et Flahault (1886, p. 338)
Syn.: Camptotrichaceae (West et West) Kirchner (1898, p. 90); Tildeniaceae Kossinskaja (1926, p. 82); Hammatoideaceae Elenkin (1949, p. 1806); Homoeothrichaceae Elenkin (1949, p. 1813); ? Sokoloviaceae Elenkin (1926, pp. 93, 95; 1949, p. 1834; cf. Geitler, 1942, p. 176)
Family Scytonemataceae Kützing ex Bornet et Flahault (1887, p. 81)
Syn.: Hydrocorynaceae Elenkin (1949, p. 991); Plectonemataceae Elenkin (1949, p. 1772); Pseudoscytonemataceae Elenkin (1949, p. 1805); Pseudodiplonemataceae Elenkin (1949, p. 1838)
Family Mastigocladaceae Geitler (1925a, p. 263)
Syn.: Lithonemataceae Elenkin (1949, p. 185)
Family Diplonemataceae (Borzi) Elenkin (1934, p. 79)
Syn.: Borzinemataceae Geitler (1942, p. 141)
Family Pulvinulariaceae Geitler (1925a, p. 254)
Syn.: Loriellaceae Geitler (1925a, p. 253)
Family Capsosiraceae Geitler (1925a, p. 255)
Syn.: Pseudocapsosiraceae Elenkin (1949, p. 1849)
Family Nostochopsidaceae Geitler (1925a, p. 257)
Syn.: ?Loefgreniaceae Elenkin (1917, p. 161; cf. Geitler, 1942, p. 135)
Family Mastigocladopsidaceae Iyengar et Desikachary (1946, p. 58)
Family Stigonemataceae Kirchner (1898, p. 80)
Syn.: Sirosiphonaceae (Stizenberger) Rabenhorst ex Engler (1892, p. 4)

Phylum Rhodophycophyta

Characterization: The algae belonging to this phylum owe their characteristic red color to the presence in their plastids of a water-soluble proteinaceous pigment (phycobilin), *r*- phycoerythrin. Some forms contain, in addition, a second water-soluble proteinaceous pigment, the blue *r*- phycocyanin. These two pigments commonly obscure the other pigments, which are: chlorophyll *a*, chlorophyll *d*, the xanthophyll lutein, alpha- and beta-carotene. A number of genera are colorless or nearly so and live as parasites on other red algae.

In the simplest red algae the thallus consists of a single cell (*Porphyridium*, *Chrootheca*). At the other extreme there are forms with a comparatively large, although never massive, foliaceous thallus (*Iridaea*, *Aeodes*). Flagellated vegetative or reproductive cells are entirely lacking in this group.

Cells of red algae have a wall that is differentiated into an inner cellulosic and an outer pectic portion. Calcification of the wall occurs in the coralline algae and in a number of other genera belonging to the orders Cryptonemiales and Nemalionales. (Encrusting coralline algae assist immensely in the building of coral reefs and often play a more important part in this process than the corals themselves. Fossil corallines are known from the Cretaceous onwards.) In primitive forms the cells are uninucleate, in others they are uni- or multinucleate, although the more highly evolved forms are always multinucleate. The reproductive organs are almost always uninucleate.

In the less specialized forms the cells usually contain a single or only a few plastids. In many of these forms the plastid is axile in position and more or less stellate in form. In the higher forms each cell usually contains several to many discoid, lenticular, or bandlike chromatophores. In the lower forms the plastids frequently contain pyrenoids which usually lack a starch sheath. The product of photosynthesis is a polysaccharide known as floridean starch.

Growth of the thallus is diffuse in the Bangiophycidae, apical or marginal in the Florideophycidae. In the latter, adjacent cells are joined by pit connections.

Sexual reproduction in the red algae is always oögamous. The female sex organ, known as the carpogonium, is usually borne at the end of a special filament, the carpogonial branch, and it usually forms a receptive process, the trichogyne. Only one egg is formed in a carpogonium. It never retracts from the carpogonial wall to become an individualized egg, either before or after fertilization. The male sex organ, or spermatangium, forms a single motionless spermatium which is conveyed passively to the trichogyne. Following its fusion with the latter, the spermatial nucleus migrates down into the carpogonium where it fuses with the egg nucleus. In the Bangiophycidae the fertilized carpogonium by division gives rise directly to a number of carposporangia. In the Nemalionales it produces gonimoblast filaments (the cystocarp) which form carposporangia. In the majority of Florideophycidae above the Gelidiales a diploid nucleus is conveyed to one or more generative auxiliary cells from which the gonimoblast is produced. In the higher groups the carpospores produce free-living tetrasporangium-forming diploid plants that resemble the sexual plants.

History: As was mentioned in the introduction to this chapter, Lamouroux (1813) was the first to remove, on the basis of color, certain red algae (11 genera) from comparable morphological types of a different color. He created a special category ("ordre") for these plants and named it Floridées. Thus Lamouroux in effect became the founder of the phylum Rhodophycophyta, although the group did not receive this status until almost a century later. The Florideae, or Florideophycidae as they should be known in conformity with the current botanical code of nomenclature, still constitute one of the two subclasses of the class Rhodophyceae.

Adopting the designation of Lamouroux, C. Agardh in 1817 made the Florideophycidae one of the five sections into which he divided the algae. Whereas Lamouroux and C. Agardh failed to distinguish sharply between green, brown, and red algae, Harvey's (1836) treatment of them in Mackay's *Flora hibernica* represents a more complete separation between these three major groups of algae. In only a few instances did he assign genera to the wrong color group.

Harvey (1836) proposed the name Rhodospermeae for the red algae, which designation was changed to Rhodophyceae by Ruprecht (1851, 1855). Kützing (1843, pp. 20, 21) suggested the names phycoerythrin and phycocyanin for the two phycobilin pigments present in the plastids of these algae. (For summaries of our knowledge of the pigments of red algae reference should be made to the reviews by Kylin, 1937a, and Strain, 1951).

Since present-day classification of the red algae is to a large degree based on the details of development of the reproductive organs, emphasis will be placed in this brief review on the growth of our knowledge of the reproductive processes of the group.

Ellis (1767) and C. Agardh (1828, pp. 57–58) referred to the clusters of spermatangia as male reproductive organs. C. Agardh used the term antheridia for those of *Polysiphonia* merely because of their superficial resemblance to an anther. That they indeed were male structures was first established by Bornet and Thuret (1866a, 1866b, 1867).

That the same species of red alga may include two kinds of plants, each with its own kind of spore-bearing structure (cystocarp and tetrasporangium) was first emphasized by Stackhouse (1801, p. xxvi). At first, Turner (1802, pp. 293–294) and others strongly opposed this view, believing that different species were involved, but later Turner (1808, p. 130) remarked about this phenomenon as follows:

> Of the zeal, with which the study of Marine Botany has been cultivated during the few years that have elapsed subsequently to the publication of the *Nereis Britannica* [by Stackhouse, 1795–1801], and the *Synopsis of the British Fuci* [by Turner, 1802], some idea may be formed from the circumstance of the double fruit of *F. [ucus] coccineus* [=*Plocamium coccineum*], being at that time regarded as a curiosity, and as so extraordinary to be in itself almost sufficient to justify the dividing of the plant into two distinct species,[12] whereas a similar appearance is now known to be observable in several of its congeners, and we have every reason to believe, that in the course of time it will be discovered in many others.

In 1847 Harvey remarked (p. 4): "The Rhodosperms are remarkable for possessing what seems to be a double system of fructification, a thing without parallel in the Vegetable Kingdom." On account of this feature, Kützing (1843) had previously named them Heterocarpeae.

Decaisne (1842a) considered the tetrasporangium as the "typical" reproductive organ of red algae and the cystocarp as a sort of proliferation or gemma. Harvey (1849, pp. 67–74), on the contrary, was of the opinion (p. 73) that the spores formed in the cystocarp should be considered ". . . of the nature of *seeds* [that is, the result of a sexual process], and not as *buds*," and that the spores formed in the tetrasporangium "should be regarded as gemmules." Because the clusters of spermatangia occur in a position similar to that of the cystocarps in many genera of red algae (on trichoblasts in the Rhodomelaceae), Harvey argued that these structures (the "antheridia" of C. Agardh) might be of the nature of stamens. In the same work he remarked, however (p. 73):

> . . . we do not yet know the cause of the formation of conceptacles [cystocarps] and the production of spores. We know that seeds result from the joint agency of stamens and

12. Turner (1802) had on this account divided it into two varieties and remarked (p. 294), "There can indeed be but little question of their being in reality separate species . . ."

pistils. But we do not know whether any process similar to fertilization takes place with the spores of these algae.

Nägeli (1847) divided the algae into two classes: (1) "Algae," which lack sexual reproduction, and (2) "Florideae," which reproduce sexually. He regarded the tetrasporangia of the Florideae as female sex organs which produce four spores, the antheridia of C. Agardh and others he considered male sex organs which produce sperms, and the cystocarps he regarded, in agreement with Decaisne, as structures of vegetative reproduction. Ruprecht (1851, pp. 205–206), on the other hand, thought the tetraspores corresponded to the pollen and the carpospores ("Samen") to the seeds of phanerogams. He thought the antheridia produced sperm cells, which were lacking in phanerogams, although this had not yet been established. It is evident that Ruprecht, like earlier botanists and those of the following fifty years, did not understand the role of the tetrasporangia in the life history of these algae.

Thuret (1851) illustrated and described in unqualified terms as antheridia, structures which he studied in several red algae and their contents as antherozooids (a term proposed by Derbès and Solier, 1850, p. 263), although he was unable actually to determine their role inasmuch as he found that both the carpospores and the tetraspores would germinate without having been in contact with the "antherozooids." Thuret's observations were confirmed by Pringsheim (1855).

Finally, Bornet and Thuret in 1866 and 1867 for the first time clearly described sexual reproduction in a number of red algae. They determined the nature of the female apparatus, which Nägeli (1861) had observed but had misinterpreted, and saw the spermatia attached to and coalescing with the trichogyne. Bornet and Thuret's discovery that the female gamete is produced in the terminal cell of a special filament, the carpogonial branch, and that this gamete is not liberated from the gametangium explained in large part why sexuality had eluded the various earlier investigators. From what was known about sexual reproduction in other groups, it was thought the female gamete would be an individualized protoplast like the egg of *Fucus* or of *Volvox*.

The observations by Bornet and Thuret were extended by themselves (1876, 1878, 1880), Solms-Laubach (1867), Janczewski (1876), Schmitz (1879b, 1883) and others. Schmitz (1883) was the first to observe that in certain red algae the fertilized carpogonium produces filaments that fuse with a neighboring cell, which he (p. 229) termed the auxiliary cell, and that the gonimoblast develops from this cell. He thought that a second fusion of nuclei occurred in the auxiliary cell and that red algae consequently showed a double fertilization. He anticipated the skepticism that his interpretation of this phenomenon would generate, for he wrote (p. 246):

Einen zweimaligen Befruchtungsact im Entwickelungskreis einer einzelnen Species anzunehmen, dagegen sträubt sich jedoch zur Zeit die botanische Anschauung völlstandig, das widerspricht aller Tradition.

Oltmanns (1898) later showed that no fusion of nuclei occurs in the auxiliary cell, which receives a fusion (diploid) nucleus from the connecting filament but whose own (haploid) nucleus migrates to one side of the cell and plays no part in the ensuing development.

Wille in 1894, working on *Nemalion,* saw the actual fusion of the male and female nuclei, an observation that was confirmed a few years later by Osterhout (1900). Yamanouchi (1906a, 1906b) first worked out the nuclear cycle and showed that the red algal genus *Polysiphonia* possesses an alternation of generations between haploid gametophytic and diploid tetrasporangial plants, with meiosis occurring in the young tetrasporangium. Thus at last was determined the long-misunderstood role of the tetrasporangia in the life history of these plants.

The correctness of Yamanouchi's observations was confirmed by Lewis (1912) by cultural studies. Svedelius (1915), studying the development and cytology of *Scinaia,* a genus which was known to lack tetrasporangia, established that in it meiosis occurs immediately after fertilization. Such species (the majority of Nemalionales) consequently lack free-living tetrasporophytes. The observations of Svedelius were quickly confirmed by Kylin (1916) and Cleland (1919). A number of Florideophycidae—members of both the Nemalionales and of some of the orders above them—were later found to have life cycles that deviate from the two general types referred to above. For a review of these the reader is referred to the papers by Drew (1944) and Papenfuss (1950b).

Oltmanns (1898, p. 138; 1904, p. 537) in agreement with Harvey (1849) and certain other early writers regarded the tetrasporangia as accessory reproductive organs. He considered the plant that produces the sex organs as the gametophyte and the gonimoblast as the sporophyte (the carposporophyte of Church, 1919b, p. 331). From the cytological work of Yamanouchi, Lewis (1909), and many later investigators, it is now well established that the majority of red algae above the Nemalionales possess three generations: a haploid gametophyte, a diploid carposporophyte which is permanently attached to and largely parasitic on the gametophyte, and a diploid, free-living tetrasporophyte. For an interesting account of the history of the discovery of an alternation of generations in the red algae the reader is referred to a paper by Svedelius (1916).

Feldmann (1952) is of the opinion that all Florideophycidae that lack a free-living tetrasporophyte are derived. Although this is unquestionably true of a number of forms—for example, certain species of *Phyllophora, Gymnogongrus,* and *Ahnfeldtia*—it may be questioned whether this is also true of those Nemalionales in which meiosis occurs immediately after fertilization (the majority of species in the order) or at carpospore formation. Svedelius (1953, p. 80, fn.) has promised to deal with this question.

Although credit must go to Lamouroux (1813) for first recognizing the red algae as an autonomous group of plants, he, like his predecessors (e.g., Gmelin, 1768), and contemporaries (e.g., Esper, 1797–1808, and Turner, 1802, 1808, 1809, 1811, 1819), did not depart from Linnaeus (1753) in classifying these algae almost entirely on their external features, even if in much greater detail than Linnaeus. This very frequently resulted in the placing together of totally unrelated forms or in the separation of related forms.

C. Agardh (1824, 1828) was the first to take into serious consideration in the classification of the algae the structure of the thallus and of the reproductive organs, even if only as regards their gross structure. With C. Agardh thus begins what Sjöstedt (1926, p. 78) has termed the anatomical period in the classification of the red algae and other groups. In the course of time, especially through the efforts of Greville (1830), Harvey (1841, 1849) and J. Agardh (1842, 1851, 1852a, 1852b, 1852c, 1863, 1872, 1876, 1879), increasing emphasis was placed on the finer details of the structure of the thallus and the reproductive organs. With the appearance of J. Agardh's work of 1842, the manner of division of the tetrasporangia, whether tetrahedral, cruciate, or zonate, was also introduced into the classification of these algae. These are characters that in general are still considered important in the delimitation of taxa.

As regards the characters offered by the structure of the cystocarp, J. Agardh's system, which was the standard one for some fifty years, took into account only the mature cystocarp. The multitude of significant characters presented by the ontogeny of this organ thus remained concealed, with the result that the system of J. Agardh, like those of his predecessors, contained a great deal that was artificial.

The present period in the classification of these algae, which Sjöstedt (1926, p. 85) has termed the embryological period, was ushered in by Schmitz's epoch-making paper of 1883. Although Nägeli (1861), Bornet and Thuret (1866a, 1866b, 1867, 1876, 1878, 1880), Solms-Laubach (1867), Janczewski (1876), and Schmitz (1879b) had worked out in some detail the development of the cystocarp, the significance of the differences in the development of this structure in different forms did not become apparent until 1883. On the basis of the fundamental differences in the ontogeny of this organ, especially as regards the place of formation and the function of the auxiliary cell, Schmitz later (1889, 1892, and in Schmitz and Hauptfleisch, 1896–1897) proposed a regrouping of these algae along lines that portrayed a much more natural arrangement than had yet been possible. Schmitz (1892) divided the Florideophycidae into the four orders Nemalionales, Gigartinales, Rhodymeniales, and Cryptonemiales.

Since comparatively few forms had been thoroughly investigated when Schmitz proposed his system, it was to be expected that further knowledge would necessitate revision of this system. Although Schmitz's four orders are still accepted, additional developmental studies have shown that they should be reconstituted and it has been necessary to create two additional orders. The first major emendation of Schmitz's system was by Oltmanns (1904), who, among other changes, erected the order Ceramiales for those Rhodymeniales of the system of Schmitz in which the auxiliary cell is formed after fertilization of the carpogonium, namely, the families Ceramiaceae, Delesseriaceae, and Rhodomelaceae (including the Dasyaceae as currently recognized). In 1923 Kylin established the order Gelidiales for the family Gelidiaceae, which Schmitz, and following him Oltmanns, had placed in the Nemalionales. Still later Kylin (1925) founded the order Nemastomales for the families Nemastomaceae and Rhodophyllidaceae (previously placed in the Cryptonemiales and Gigartinales, respectively) and Sjöstedt (1926) erected the order Sphaerococcales for the family Sphaerococcaceae (previously placed in the Gigartinales), but these two orders were subsequently reduced by Kylin (1928, p. 113; 1932, pp. 71, 72, 76–79) under the Gigartinales. Recently Feldmann (1952) established an order Bonnemaisoniales. Although the genera comprising this order do not appear to be closely related to the other members of the Nemalionales (in which order the Bonnemaisoniaceae have been placed in recent times), the points of departure do not seem to be of sufficient magnitude to justify recognition of a separate order.

Oltmanns (1904) brought into focus an anatomical character that has proved of great importance in the classification of the Florideophycidae. He emphasized that in some genera the thallus has a uniaxial construction whereas in others it is multiaxial. Kylin (1928, 1930a, and especially 1932) has made very effective use of this character in the separation of families.

We are especially indebted to Kylin for the refinement of Schmitz's embryological system of classification of the Florideophycidae. In a long series of papers, especially the monographic studies of 1923, 1928, 1930a, and 1932, he has immensely advanced our knowledge of the comparative morphology of these algae and has thereby contributed more than any other one person to a better understanding of the interrelationships of this large and diversified phylum. Despite certain shortcomings (see Papenfuss, 1951b) his system of 1932 allows of a much more natural arrangement than had previously been possible. It is the standard one today.

In Kylin's system the orders are separated on whether or not "typical" auxiliary cells (generative auxiliary cells of Papenfuss, 1951b) are absent or present, their time of formation—before or after fertilization—and their manner and place of formation. Within the orders, the families are separated on whether the thallus is uniaxial or multiaxial, whether the cystocarp is imbedded in the thallus or not, whether the tetrasporangia are tetrahedrally, cruciately, or zonately divided, and various other characters of seemingly comparable importance.

In regard to the long-standing disagreement between Svedelius and Kylin as to whether the Nemalionales do or do not possess a "typical" auxiliary cell reference should be made to the papers by Martin (1939), Svedelius (1942), and Kylin (1944b). In the opinion of Kylin, the cell or cells in the nemalionalean carpogonial branch that receive a diploid nucleus from the fertilized carpogonium and from which the gonimoblast develops do not constitute a "typical" auxiliary cell; yet he has no hesitation in considering the supporting cell in the Kallymeniaceae (Cryptonemiales) and in *Sphaerococcus* (Gigartinales) as a "typical" auxiliary cell, even though it is a cell in the carpogonial branch system.

Brief mention should be made of two groups of red algae which at first were not associated with this phylum. The first of these, the Corallinaceae, were for a long time, along with other calcified algae, regarded as corals. S. F. Gray (1821) appears to have been the first botanist to have considered them algae, without qualification, but they did not receive general acceptance as red algae until Decaisne (1842b) showed that they possess the typical features of this group.

Despite their purple color the members of the other group, the subclass Bangiophycidae, were for many decades after they had become known classified with the filamentous or membranous green algae which they resemble in habit. As recently as 1922 Oltmanns (1922b, p. 230) stated that he was not fully convinced that these forms really belong with the Rhodophyceae. Although Thuret (*in* Le Jolis, 1863) and Rabenhorst (1868) had associated these forms with the Rhodophyceae, their place among the latter remained uncertain until the appearance of Berthold's (1881a, 1882) critical investigations of various members of the group.

Phylogenetically, the red algae appear to be distantly related to the blue-green algae by way of the Bangiophycidae. Cohn (1867) was the first to arrive at this conclusion on the basis of his investigation of the pigments of both groups. Such a relationship appeared likely to Berthold (1882) also and is accepted by Ishikawa (1921, 1924), Kylin (1930b, 1937a, 1943b), Tilden (1933, 1935) and Skuja (1938).

In the synoptic outline that follows, Skuja's (1939a) classification of the Bangiophycidae (which has been accepted by Kylin, 1944a, and Tanaka, 1952) has been followed. The classification of the Florideophycidae is essentially that of Kylin (1932).

Phylum RHODOPHYCOPHYTA Papenfuss (1946, p. 218)
- Syn.: Rhodophyta Wettstein (1901, p. 46)
  - Class RHODOPHYCEAE Ruprecht (1851, p. 205)
    - Syn.: Rhodospermeae Harvey (1836, p. 160); Heterocarpeae Kützing (1843, p. 369); Phycoérythrinophycées Marchand (1895, p. 17)
    - Subclass BANGIOPHYCIDAE De Toni orth. mut. L. M. Newton (1953, p. 406)
      - Syn.: Bangioideae De Toni (1897, p. 4); Protoflorideae Rosenvinge (1909, p. 55)
      - Order PORPHYRIDIALES Kylin (1937b, p. 4; see also Kylin, 1937a, pp. 39–51)
        - Family Porphyridiaceae Kylin (1937b, p. 4)
      - Order GONIOTRICHALES Skuja (1939a, p. 31)
        - Family Goniotrichaceae (Rosenvinge) Skuja (1939a, p. 31)
        - Family Phragmonemataceae Skuja (1939a, p. 32)
      - Order BANGIALES Engler (1892, p. 15)
        - Family Erythropeltidaceae Skuja (1939a, p. 33)
        - Family Bangiaceae (S. F. Gray) Nägeli (1847, p. 136)
          - Syn.: Porphyraceae Kützing orth. mut. Rabenhorst (1868, p. 397); Erythrotrichiaceae Marchand orth. mut. G. M. Smith (1944, p. 162)
      - Order RHODOCHAETALES Skuja (1939a, p. 34)
        - Family Rhodochaetaceae Schmitz, *in* Schmitz and Hauptfleisch (1896, p. 317)
      - Order COMPSOPOGONALES Skuja (1939a, p. 34)
        - Family Compsopogonaceae Schmitz, *in* Schmitz and Hauptfleisch (1896, p. 318)
    - Subclass FLORIDEOPHYCIDAE (Lamouroux) Engler orth. mut. L. M. Newton (1953, p. 407)
      - Syn.: Floridées Lamouroux (1813, p. 115); Euflorideae Johnson (1894, p. 639)
      - Order NEMALIONALES Schmitz, *in* Engler (1892, p. 17)
        - Syn.: Bonnemaisoniales Feldmann (1952, p. 29)
        - Family Acrochaetiaceae Fritsch (1944, p. 258)
          - Syn.: Chantransiaceae Kützing orth. mut. Rabenhorst (1868, p. 400; not including *Chantransia* De Candolle, see Silva, 1952, pp. 261–262); Rhodochortonaceae Nasr (1947, p. 92)
        - Family Batrachospermaceae (C. Agardh) Dumortier orth. mut. Rabenhorst (1868, p. 404)
        - Family Lemaneaceae (S. F. Gray) Harvey orth. mut. Rabenhorst (1863, p. 275)
        - Family Helminthocladiaceae (J. Agardh) Harvey orth. mut. Hauck (1883, p. 14)
          - Syn.: Nemalionaceae Cohn orth. mut. G. Murray (1895, p. 207)
        - Family Chaetangiaceae Kützing orth. mut. Hauck (1883, p. 14)
        - Family Thoreaceae Reichenbach ex Hassall orth. mut. Schmitz, *in* Schmitz and Hauptfleisch (1896, p. 321)
        - Family Naccariaceae Kylin (1928, p. 11)
        - Family Bonnemaisoniaceae Schmitz, *in* Engler (1892, p. 20)

Order GELIDIALES Kylin (1923, p. 132)
  Family Gelidiaceae Kützing orth. mut. Harvey (1853, p. 7)
Order CRYPTONEMIALES Schmitz, *in* Engler (1892, p. 21)
  Family Dumontiaceae Bory orth. mut. Schmitz (1889, p. 453)
  Family Rhizophyllidaceae Montagne orth. mut. Schmitz (1889, p. 454)
  Family Polyideaceae Kylin (1944a, p. 34)
    Syn.: Spongiocarpeae Greville (1830, p. 68)
  Family Squamariaceae (J. Agardh) Hauck (1883, p. 13)
  Family Solenoporaceae Pia (1927, p. 97)
  Family Hildenbrandiaceae (Trevisan) Rabenhorst (1868, p. 408)
  Family Corallinaceae (Lamouroux) Harvey (1849, p. 74)
  Family Gloiosiphoniaceae Schmitz, *in* Engler (1892, p. 21)
  Family Dermocorynidaceae Hollenberg (1940, p. 871)
  Family Endocladiaceae (J. Agardh) Kylin (1928, p. 41)
  Family Tichocarpaceae (Schmitz) Kylin (1932, p. 69)
  Family Cryptonemiaceae (J. Agardh) Harvey (1849, p. 75; see also Hauck, 1883, p. 16)
    Syn.: Grateloupiaceae Schmitz, *in* Engler (1892, p. 21)
  Family Kallymeniaceae (J. Agardh) Funk (1927, p. 389)
  Family Choreocolacaceae Sturch (1926, p. 602)
Order GIGARTINALES Schmitz, *in* Engler (1892, p. 18)
  Syn.: Nemastomales Kylin (1925, p. 39); Sphaerococcales Sjöstedt (1926, p. 75)
  Family Cruoriaceae (J. Agardh) Kylin (1928, p. 29)
  Family Calosiphoniaceae Kylin (1932, p. 5)
  Family Nemastomaceae (J. Agardh) Schmitz (1889, p. 453)
    Syn.: Gymnophlaeaceae Kützing (1843, p. 389); Yadranellaceae Ercegović (1949, p. 36). The latter family is placed here at the suggestion of Dr. Isabella Abbott, personal communication.
  Family Furcellariaceae Greville orth. mut. Kylin (1932, p. 11)
  Family Sebdeniaceae Kylin (1932, p. 12)
  Family Solieriaceae (Harvey) Hauck (1883, p. 17)
  Family Rissoëllaceae (J. Agardh) Kylin (1932, p. 31)
  Family Rhabdoniaceae Kylin (1925, p. 38)
  Family Rhodophyllidaceae Schmitz, *in* Engler (1892, p. 19)
  Family Hypneaceae J. Agardh (1852, p. 430)
  Family Plocamiaceae Kützing orth. mut. Kylin (1930, p. 45)
  Family Sphaerococcaceae Dumortier orth. mut. Cohn (1872a, p. 17)
  Family Stictosporaceae Kylin (1932, p. 53)
  Family Sarcodiaceae Kylin (1932, p. 54)
  Family Gracilariaceae (Nägeli) Kylin (1930a, p. 54)
  Family Mychodeaceae (Schmitz et Hauptfleisch) Kylin (1932, p. 62)
  Family Dicranemaceae (Schmitz et Hauptfleisch) Kylin (1932, p. 65)
  Family Acrotylaceae Schmitz, *in* Engler (1892, p. 18)
  Family Phyllophoraceae Nägeli (1847, p. 248)
  Family Gigartinaceae Bory orth. mut. Cohn (1880, p. 286)
  Family Chondriellaceae Levring (1941, p. 640)
Order RHODYMENIALES Schmitz, *in* Engler (1892, p. 19)
  Family Rhodymeniaceae Harvey (1849, p. 75)
  Family Champiaceae Kützing orth. mut. Bliding (1928, p. 64)
    Syn.: Lomentariaceae Nägeli (1847, p. 244)
Order CERAMIALES Oltmanns (1904, p. 683)
  Family Ceramiaceae (S. F. Gray) Harvey orth. mut. Rabenhorst (1847, p. xiii)
    Syn.: Wrangeliaceae J. Agardh orth. mut. Harvey (1853, p. 8); Spyridiaceae J. Agardh orth. mut. Harvey (1853, p. 8)
  Family Dasyaceae Kützing orth. mut. Rosenberg (1933, p. 83)
  Family Delesseriaceae Bory orth. mut. Nägeli (1847, p. 208)

Family Rhodomelaceae (J. Agardh) Harvey (1849, p. 74)
Syn.: Laurenciaceae Harvey (1849, p. 74); Rytiphlaeaceae Kützing (1843, p. 442)

Prospect

From the preceding review it will be evident that knowledge of the structure and reproduction of the algae, and hence of their classification, has advanced tremendously during the past hundred years. It is now well established that the assemblage of plants referred to as algae is comprised of a number of only distantly related groups of organisms that share few characters except the ability of most of the forms to synthesize organic compounds by the process of photosynthesis and the absence of a primarily produced jacket of sterile cells about the reproductive organs.

If the bases of the present systems of classification of the members of the major groups are examined, however, it is found that not infrequently families and even orders have been established on the strength of knowledge obtained from a study of only a few species or in certain instances only one species. Obviously there exists a great need for detailed information on a large number of genera and species before it will be possible to erect schemes of classification that will portray in a reasonably accurate way the phylogenetic affinities of the organisms that constitute these groups. It is no exaggeration to say that only a good beginning has been made in the sorting out of the natural subdivisions of the major taxa.

Biochemical information has contributed much to a better understanding of the interrelationships of various groups of algae. It is to be expected that biochemical investigation of the many forms that have not yet received attention will yield knowledge that will be as significant as that obtained in the past.

Although the chromosomes of algae are generally small and hence do not lend themselves well to karyological study, cytotaxonomic investigations like those of Cave and Pocock (1951) encouragingly point to the rich rewards that may be expected from the pursuit of problems in this largely unexplored area.

In recent years electron microscope studies have yielded valuable information on the structure of the flagella and the cell wall of diverse algae. The interesting new facts brought to light augur well for an expanding use of this tool in algal research.

In the past, knowledge of the developmental morphology and the life histories of algae has contributed greatly toward the elucidation of phylogenetic affinities among these plants. Pressing needs exist for information of this kind on many more species. In numerous instances progress in life-history studies has been greatly retarded and not infrequently the results have been woefully fragmentary owing to the difficulty of obtaining germination stages of the zygospores or other resting cells. It may be anticipated that in the future the physiology of resting cell maturation and germination will receive the attention that it merits and that the knowledge gained will make it possible to induce these cells to mature and germinate at will. An understanding of the physiology of resting cell germination will not only aid in life-history studies but will be a tremendous impetus to the full utilization of these simple autotrophic plants as material in experimental studies.

With the expanding use of algae as experimental material we may look forward to an increasing awareness among biologists in general of the need for precise identity of the forms under investigation. It may be anticipated therefore that the preservation of voucher collections of published material will become standard practice and that the maintenance and welfare of such repositories as herbaria, museums, and living culture collections will be the concern and the accepted responsibility, not only of the taxonomist and morphologist, but of all biologists.

LITERATURE CITED

Adanson, M.

1763. Familles des plantes. Pt. 2. (1)–(18) + 640 + (19)–(24) pp. Paris: Vincent.

Agardh, C. A.

1817. Synopsis algarum scandinaviae . . . xl + 135 pp. Lund: Officina Berlingiana.

1824. Systema algarum. xxxviii + 312 pp. Lund: Literis Berlingianis.

1828. Species algarum . . . Vol. 2(1). lxxvi + 189 pp. Greifswald: Moritz.

1830–1832. Conspectus criticus diatomacearum . . . 66 pp. Lund: Literis Berlingianis.

Agardh, J. G.

1842. Algae maris mediterranei et adriatici . . . x + 164 pp. Paris: Masson.

1848. Species genera et ordines algarum . . . Vol. 1. viii + 363 pp. Lund: Gleerup.

1851. Species genera et ordines algarum . . . Vol. 2(1). xii + 336 + [addenda and index] 337–351 pp. Lund: Gleerup.

1852a. Species genera et ordines algarum . . . Vol. 2(2:1). Pp. 337–504. Lund: Gleerup.

1852b. Species genera et ordines algarum . . . Vol. 2(2:2). Pp. 505–700 + [addenda and index] 701–720. Lund: Gleerup.

1852c. Species genera et ordines algarum . . . Vol. 2 (3:1). Pp. 701–786. Lund: Gleerup.

1863. Species genera et ordines algarum . . . Vol. 2(3:2). Pp. 787–1291. Lund: Gleerup.

1872. Bidrag till florideernes systematik. Lunds Univ. Årsskr. Afd. 2, 8(6). 60 pp.

1876. Species genera et ordines algarum . . . Vol. 3(1). Epicrisis systematis floridearum. vii + 724 pp. Leipzig: Weigel.

1879. Florideernes morphologi. K. Svensk. Vet.-Akad. Handl., 15(6). 199 pp., 33 pls.

1887–1888. Till algernes systematik . . . (Afd. 5). Lunds Univ. Årsskr. Afd. 3, 23(2). 174 pp., pls. 1–5.

Allen, C. E.

1905. Die Keimung der Zygote bei *Coleochaete*. Ber. Deutsch. Bot. Ges., 23:285–292, pl. 13.

Allman, G. J.

1855. Observations on *Aphanizomenon Flos-a-quae*, and a species of *Peridinea*. Quart. Journ. Micr. Sci., 3:21–25, pl. 3.

1872. Notes on *Noctiluca*. Quart. Journ. Micr. Sci., n. s., 12:326–332, pl. 18.

Allorge, P.

1930. Hétérocontes ou Xanthophycées? Rev. Alg., 5(2):230.

Arasaki, S.

1949. On the life-history and the systematical position of *Dictyosiphon foeniculaceus* (Huds.) Grev. Bot. Mag. Tokyo, 62:87–90, 3 figs.

ARESCHOUG, J. E.

1847. Phycearum, quae in maribus scandinaviae crescunt, enumeratio. Sectio prior, Fucaceas continens. Nova Acta Reg. Soc. Sci. Upsal., ser. 2, 13:223–382 + [1], pls. 1–9.

ATKINSON, G. F.

1905. A College Text-Book of Botany . . . , 2nd ed. xvi + 737 pp., 592 figs., frontis. New York: Holt and Co.

BARY, A. DE

1854. Ueber die Algengattungen *Oedogonium* und *Bolbochaete*. Abhl. Senckenberg. Naturforsch. Ges., 1:29–105, pls. 2–4.

1858a. Über den geschlechtlichen Zeugungsprozess bei den Algen. Ber. Verhl. Ges. Förderung Naturwiss. Freiburg i. Br., 1856:215–230, pl. 5. (Not seen, cited from Kniep, 1928.)

1858b. Untersuchungen über die Familie der Conjugaten (Zygnemeen und Desmidieen). Ein Beitrag zur physiologischen und beschriebenden Botanik. [4] + 91 pp., 8 pls. Leipzig: Förstnersche Buchhandlung.

1872. Über den Befruchtungsvorgang bei den Charen. Monatsber. K. Preuss. Akad. Wiss. Berlin, 1871:227–239, 1 pl.

1875. Zur Keimungsgeschichte der Charen. Bot. Zeit., 33:377–385, 393–401, 409–420, pls. 5, 6.

1881. Zur Systematik der Thallophyten. Bot. Zeit., 39:1–17, 33–36.

BEHLAU, J.

1935. Die Spondylomoraceen-Gattung *Chlamydobotrys*. Beitr. Biol. Pflanz., 23:125–166, 7 figs., 4 tables, pl. 3.

1939. Der Generationswechsel zwischen *Chlamydomonas variabilis* Dangeard und *Carteria ovata* Jacobsen. Beitr. Biol. Pflanz., 26:221–249, 3 figs.

BENNETT, A. W.

1878. On the structure and affinities of Characeae. Journ. Bot. 16:202–207.

1879. A few last words on *Chara*. Journ. Bot. 17:67–69.

BERGH, R. S.

1881. Der Organismus der Cilioflagellaten. Eine phylogenetische Studie. Morph. Jahrb., 7(2):177–288, pls. 12–16.

BERGMANN, C., and R. LEUCKART

1852. Anatomisch-physiologische Uebersicht des Thierreichs. xii + 690 + [2] pp., 438 figs. Stuttgart: Müller's Verlagshandlung.

BERTHOLD, G.

1881a. Zur Kenntnis der Siphoneen und Bangiaceen. Mitt. Zool. Stat. Neapel, 2:72–82.

1881b. Die geschlechtliche Fortpflanzung der eigentlichen Phaeosporeen. Mitt. Zool. Stat. Neapel, 2:401–413, pl. 17.

1822. Die Bangiaceen des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Fauna Flora Golfes Neapel, 8. [4] + 28 pp., 1 pl.

BISCHOFF, G. W.

1828. Die kryptogamischen Gewächse . . . x + 131 pp., 13 pls. Nürnberg: Schrag.

BLACKBURN, KATHLEEN B.

1936. A reinvestigation of the alga *Botryococcus Braunii* Kützing. Trans. Roy. Soc. Edinburgh, 58(3):841–854, 4 figs., pl. 1.

BLACKMAN, F. F.

1900. The primitive algae and the Flagellata. An account of modern work bearing on the evolution of the algae. Ann. Bot., 14:647–688, figs. 13, 14.

BLACKMAN, F. F., and A. G. TANSLEY
1902. A revision of the classification of the green algae. New Phytol., 1:17–24, 47–48, 67–72, 89–96, 114–120, 133–144, 163–168, 189–192, 213–220, 238–244.

BLIDING, C.
1928. Studien über die Florideenordnung Rhodymeniales. Lunds Univ. Årsskr., N. F., Avd. 2, 24(3). 74 pp., 52 figs.

BOHLIN, K.
1897a. Studier öfver några slägten af alggruppen Confervales Borzi. Bihang K. Svensk. Vet.-Akad. Handl. 23, Afd. 3, No. 3. 56 pp., 2 pls.
1897b. Zur Morphologie und Biologie einzelliger Algen. (Vorläufige Mitteilung.) öfvers. K. [Svensk.] Vet.-Akad. Förhandl. 1897:507–529, 10 figs.
1901. Utkast till de gröna algernas och arkegoniaternas fylogeni. 43 + iv pp., 1 folding chart. Thesis. Lund: Publ. by author.

BONNEMAISON, T.
1822. Essai d'une classification des hydrophites loculées, ou plantes marines articulées qui croissent en France. Journ. Phys., Chimie, Hist. Nat. et Arts, 94:138–148 (Mars), 174–203 (Avril).

BONPLAND, A., and F. H. A. VON HUMBOLDT
1815. Nova genera et species plantarum . . . Tome 1. lviii + 377 pp., 96 pls. Paris: Publ. by authors?

BORGE, O., and A. PASCHER
1913. Zygnemales. *In* Pascher, Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz, Heft 9. iv + 51 pp., 79 figs. Jena: G. Fischer.

BORGERT, A.
1891. Über die Dictyochiden, insbesondere über *Distephanus speculum;* sowie Studien an Phaeodarien. Zeitschr. Wiss. Zool., 51:629–676, 2 figs., pl. 33.

BØRGESEN, F.
1905. Contributions a la connaissance du genre *Siphonocladus* Schmitz. Overs. K. Dansk. Vidensk. Selsk. Forhandl., 1905:259–291, 13 figs.
1913. The marine algae of the Danish West Indies. Part 1. Chlorophyceae. Dansk Bot. Arkiv 1(4). 158 + [2] pp., 126 figs., 2 maps.
1925. Marine algae from the Canary Islands . . . I. Chlorophyceae. K. Dansk. Vidensk. Selsk. Biol. Meddel., 5(3). 123 pp., 49 figs.

BORNET, É.
1891. Note sur quelques *Ectocarpus.* Bull. Soc. Bot. France, 38:353–372, pls. 6–8.

BORNET, É., and C. FLAHAULT
1886–1888. Revision des Nostocacées hétérocystées contenues dans les principaux herbiers de France. Ann. Sci. Nat. Bot., sér 7, 3:323–381 (1886); 4:343–373 (1886); 5:51–129 (1887); 7:177–262 (1888).

BORNET, É., and G. THURET
1866a. Sur la fécondation des Floridées. Compt. Rend. Acad. Sci. [Paris], 63:444–447.
1866b. Note sur la fécondation des Floridées. Mém. Soc. Imp. Sci. Nat. Cherbourg, 12:257–262.
1867. Recherches sur la fécondation des Floridées. Ann. Sci. Nat. Bot., sér. 5, 7:137–166, pls. 11–13.
1876. Notes algologiques . . . , fasc. 1. xx + 1–70 + [2] pp., pls. 1–25. Paris: Masson.
1880. Notes algologiques . . . , fasc. 2. Pp. 71–196, pls. 26–50. Paris: Masson.

Borzi, A.

1878. Note alla morfologia e biologia delle alghe ficocromacee. Nuova Giorn. Bot. Ital., 10:236–288, pls. 7–10.

1879. Note alla morfologia e biologia delle alghe ficocromacee. Nuovo Giorn. Bot. Ital., 11:347–388, pls. 9–12.

1882. Note alla morfologia e biologia delle alghe ficocromacee. Nuovo Giorn. Bot. Ital., 14:272–315, pls. 16, 17.

1889. *Botrydiopsis* nuovo genere di alghe verdi. Boll. Soc. Ital. Microscop., 1:60–70.

1895. Studi algologici . . . , fasc. 2. Pp. [i–vii], 121–378, pls. 10–31. Palermo: Reber.

1914. Studi sulle mixoficee. Nuovo Giorn. Bot. Ital., ser. 2, 21:307–360.

1916. Studi sulle mixoficee. Nuovo Giorn. Bot. Ital., ser. 2, 23:559-588, 6 figs.

1917. Studi sulle mixoficee. Nuovo Giorn. Bot. Ital., ser. 2, 24:17–30, 65–112, 198–214, pls. 6–10.

Braun, A.

1849. Uebersicht der schweizerischen Characeen. Ein Beitrag zur Flora der Schweiz. Neue Denkschr. Allg. Schweiz. Ges. Gesammt. Naturwiss., 10 (Art. 4). 23 pp.

1851. Betrachtungen über die Erscheinung der Verjüngung in der Natur, insbesondere in der Lebens- und Bildungs-geschichte der Pflanze. xvi + 363 pp., 3 pls. Leipzig: W. Engelmann.

1852. Über die Richtungsverhältnisse der Saftströme in den Zellen der Characeen. Ber. Verh. K. Preuss. Akad. Wiss. Berlin, 1852:220–268.

1853. Über die Richtungsverhältnisse der Saftströme in den Zellen der Characeen (Fortsetzung und Schluss). Ber. Verh. K. Preuss. Akad. Wiss. Berlin, 1853: 45–76.

1855. Algarum unicellularium genera nova et minus cognita. [6] + 111 pp., 6 pls. Leipzig: W. Engelmann.

Braun, A., and O. Nordstedt

1883. Fragmente einer Monographie der Characeen. Abh. K. Akad. Wiss. Berlin, 1882 (Article 1). 211 pp., 7 pls.

Brown, H. P.

1945. On the structure and mechanics of the protozoan flagellum. Ohio Journ. Sci., 45:247–278, pls. 1–12.

Brunnthaler, J.

1913. Die systematische Gliederung der Protococcales (Chlorophyceae). Verh. Zool.-Bot. Ges. Wien, 63:76–91.

1915. Protococcales. *In* A. Pascher, Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz, Heft 5: Chlorophyceae II. Pp. 52–205, 330 figs. Jena: G. Fischer.

Bütschli, O.

1883–1887. Protozoa. Abt. 2, Mastigophora. *In* H. G. Bronn's Klassen und Ordnungen des Thier-Reichs . . . Bd. 1. Pp. [3], 617–1097, pls. 39–55. Leipzig and Heidelberg: Winter'sche Verlagshandlung.

1885. Einige Bemerkungen über gewisse Organisations-verhältnisse der sog. Cilioflagellaten und der *Noctiluca*. Morph. Jahrb. 10:529–577, 4 figs., pls. 26–28.

Calvin, M., and V[ictoria] Lynch

1952. Grana-like structures of *Synechococcus cedorum*. Nature, 169:455–456, 2 figs.

Carter, H. J.

1856. Notes on the freshwater Infusoria of the Island of Bombay. No. 1. Organization. Ann. Mag. Nat. Hist., ser. 2, 18:115–132, 221–249, pls. 5–7.

1858. Note on the red colouring matter of the sea 'round the shores of the Island of Bombay. Ann. Mag. Nat. Hist., ser. 3, 1:258–262.

CARTER, NELLIE

1937. New or interesting algae from brackish water. Archiv Protistenk. 90(1):1–68, 3 figs., pls. 1–8.

CAVE, MARION S., and MARY A. POCOCK

1951. Karylogical studies in the Volvocaceae. Amer. Journ. Bot., 38:800–811, 47 figs., 2 tables.

CHADEFAUD, M.

1945. Sur la position systématique des Vauchéries. Bull. Soc. Bot. France, 92:47–50.

1950a. Les cellules nageuses des algues dans l'embranchement des Chromophycées. Compt. Rend. Acad. Sci. [Paris], 231:788–790, 7 figs.

1950b. Les cellules nageuses des algues dans l'embranchement des Chlorophycées. Compt. Rend. Acad. Sci. [Paris], 231:988–990, 7 figs.

CHAPMAN, V. J.

1952. New entities in the Chlorophyceae of New Zealand. Trans. Roy. Soc. New Zealand, 80:47–58, 12 figs., pls. 21, 22.

CHATTON, É

1920. Les péridiniens parasites morphologie, reproduction, ethologie. Arch. Zool. Expériment. Gén., 59:1–475, 161 figs., 18 pls.

CHODAT, R.

1902. Algues vertes de la Suisse. Pleurococcoïdes-Chroolépoïdes. Beitr. Krypt.-flora Schweiz, 1(3). xiii + 373 pp., 264 figs.

1909. Étude critique et expérimentale sur le polymorphisme des algues. 165 + [1] pp., pls. 1–21, A–B. Geneva: Georg and Co.

1921. Matériaux pour l'histoire des algues de la Suisse. IV. Sur le groupe provisoire des Chrysostomatacées. Bull. Soc. Bot. Genève, sér. 2, 13:81–87, figs. 8–10.

CHOLNOKY, B. VON

1928. Über die Auxosporenbildung der *Anomoeoneis sculpta* E. Cl. Archiv Protistenk., 63:23–57, pls. 3–6.

1933a. Beiträge zur Kenntnis der Karyologie der Diatomeen. Archiv Protistenk., 80:321–348, 41 figs.

1933b. Die Kernteilung von *Melosira arenaria* nebst einigen Bemerkungen über ihre Auxosporenbildung. Zeitschr. Zellforsch. Mikr. Anat., 19:698–719, 24 figs.

CHURCH, A. H.

1919a. Historical review of the Phaeophyceae. Journ. Bot., 57:265–273.

1919b. Historical review of the Florideae.—I. Journ. Bot., 57:297–304. [The same]—II. *Ibid.*: 329–334.

CIENKOWSKI, L.

1865a. Ueber einige chlorophyllhaltige Gloeocapsen. Bot. Zeit., 23:21–27, pl. 1.

1865b. Beiträge zur Kenntniss der Monaden. Archiv Mikr. Anat., 1:203–232, pls. 12–14.

1870. Ueber Palmellaceen und einige Flagellaten. Archiv Mikr. Anat., 6:421–438, pls. 23, 24.

CLAPARÈDE, E., and J. LACHMANN

1858–1859. Études sur les infusoires et les Rhizopodes. Vol. 1. Mém. Inst. Genevois, Vols. 5 and 6. 482 pp., 24 pls.

CLELAND, R. E.

1919. The cytology and life history of *Nemalion multifidum*, Ag. Ann. Bot., 33:323–351, 3 figs., pls. 22–24.

COHN, F.

1852. Ueber eine neue Gattung aus der Familie der Volvocinen. Zeitschr. Wiss. Zool., 4(1):77–116, pl. 6.

1853. Beiträge zur Entwickelungsgeschichte der Infusorien. II. Ueber den Encystirungsprocess der Infusorien. Zeitschr. Wiss. Zool., 4(3–4):253–281, pl. 13.

1854. Untersuchungen über die Entwickelungsgeschichte der mikroskopischen Algen und Pilze. Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Curios., 24:103–256, pls. 15–20.

1855. Über die Fortpflanzung von *Sphaeroplea annulina*. Ber. Verh. K. Preuss. Akad. Wiss. Berlin, 1855:335–351.

1856. Observations sur les Volvocinées, et spècialement sur l'organisation et la propagation du *Volvox globator*. Ann. Sci. Nat. Bot., sér. 4, 5:323–332.

1867. Beiträge zur Physiologie der Phycochromaceen und Florideen. Archiv Mikr. Anat., 3:1–60, pls. 1, 2.

1872a. Conspectus familiarum cryptogamarum secundum methodum naturalem dispositarum. Hedwigia, 11:17–20.

1872b. Grundzüge einer neuen natürlichen Anordnung der kryptogamischen Pflanzen. Jahres-Ber. Schles. Ges. Vaterl. Cultur, 49:83–89.

1880. Über sein Thallophytensystem. Jahres-Ber. Schles. Ges. Vaterl. Cultur, 57: 279–289.

CONRAD, W.

1914. Contributions à l'étude des flagellates: III. La morphologie et la nature des enveloppes chez *Hymenomonas roseola* Stein et *H. coccolithophora* Massart et Conrad, nov. spec., et les Coccolithophoridae. Ann. Biol. Lacustre, 7:155–164, 6 figs.

1926. Recherches sur les Flagellates de nos eaux saumâtres. 2e Partie: Chrysomonadines. Archiv Protistenk., 56:167–231, 28 figs., pls. 7–9.

1927. Essai d'une monographie des genres *Mallomonas* Perty (1852) et *Pseudomallomonas* Chodat (1920). Archiv Protistenk., 59:423–505, 42 figs., pls. 8–11.

1928. Le genre *Microglena* C. G. Ehrenberg (1838). Archiv Protistenk., 60:415–439, 13 figs.

1933. Revision du genre *Mallomonas* Perty (1851) incl. *Pseudomallomonas* Chodat (1920). Mém. Mus. Roy. Hist. Nat. Belgique, No. 56. 82 pp., 70 figs.

COPELAND, J. J.

1936. Yellowstone thermal Myxophyceae. Ann. New York Acad. Sci., 36:i–vi, 1–229, 73 figs.

CZURDA, V.

1932. Zygnemales [second treatment]. *In* A. Pascher, Die Süsswasser-Flora Mitteleuropas. Heft 9. iv + [1] + 232 pp., 226 figs. Jena: G. Fischer.

1937. Conjugatae. *In* K. Linsbauer, Handbuch der Pflanzenanatomie. Abt. II, Bd. 6(2): Algen B:b. [2] + 176 pp., 124 figs. Berlin: Gebr. Borntraeger.

DALECHAMPS, J.

1587. Historia generalis plantarum, . . . Vol. 1. [10] + 1095 pp., illus. with unnumbered text figs. Lyons: Rovillius.

DANGEARD, P.

1937. Notice sur la vie et les travaux de Camille Sauvageau (1861–1936). Bull. Stat. Biol. Arcachon, 34:5–57, portr.

DANGEARD, P. A.

1889. Recherches sur les Cryptomonadinae et les Euglenae. Botaniste, 1:1–38, pl. 1.

DECAISNE, J.

1842a. Essai sur une classification des algues et des polypiers calcifères de Lamouroux. Ann. Sci. Nat. Bot., sér. 2, 17:297–380, pls. 14–17.

1842b. Mémoire sur les corallines ou polypiers calcifères. Ann. Sci. Nat. Bot., sér. 2, 18:96–128.

DEFLANDRE, G.

1934. Sur la structure des flagelles. Ann. Protistol., 4:31–54, pls. 1–5.

DERBÈS, A., and A. J. J. SOLIER

1850. Sur les organes reproducteurs des algues. Ann. Sci. Nat. Bot., sér. 3, 14:261–282, pls. 32–37.

DESIKACHARY, T. V.

1952. Electron microscope study of the diatom-wall structure. Journ. Sci. Indus. Res. 11B(11):491–500, 28 figs.

DIESING, K. M.

1866. Revision der Prothelminthen. Abtheilung: Mastigophoren. Sitzungsber. Math.-Naturwiss. Cl. K. Akad. Wiss. Wien, 52 Abt. 1:287–401.

DILLWYN, L. W.

1802–1809. British Confervae; or Colored Figures and Descriptions of the British Plants Referred by Botanists to the Genus *Conferva*. [2] + 87 + [231] pp., pls. 1–109, A–G. London: Phillips.

DIWALD, K.

1938. Die ungeschlechtliche und geschlechtliche Fortpflanzung von *Glenodinium lubiniensiforme* spec. nov. Flora, 132:174–192, 4 figs., 5 tables.

DOFLEIN, F.

1922. Untersuchungen über Chrysomonadinen. Archiv Protistenk., 44(2):149–213, 4 figs., pls. 6–10.

1923. Untersuchungen über Chrysomonaden. III and IV. Archiv Protistenk., 46:267–344, 7 figs., pls. 15–22.

1928. Lehrbuch der Protozoenkunde . . . 5th ed. (E. Reichenow, ed.), Teil 2, Spezielle Naturgeschichte der Protozoen, Erste Hälfte: Mastigophoren und Rhizopoden. Pp. 439–862, figs. 389–823. Jena: G. Fischer.

DREW, KATHLEEN M.

1944. Nuclear and somatic phases in the Florideae. Biol. Rev., 19:105–120, 6 figs.

DROUET, F.

1951. Cyanophyta. *In* G. M. Smith, ed., Manual of Phycology . . . Pp. 159–166. Waltham, Mass.: Chronica Botanica Co.

DROUET, F., and A. COHEN

1935. The morphology of *Gonyostomum semen* from Woods Hole, Massachusetts. Biol. Bull., 68:422–439, 2 pls.

1937. Further observations on *Gonyostomum semen*. Bot. Gaz., 98:617–618, 1 fig.

DROUET, F., and W. A. DAILY

1952. A synopsis of the coccoid Myxophyceae. Butler Univ. Bot. Studies, 10:220–223.

DUJARDIN, F.

1841. Histoire naturelle des zoophytes. Infusoires, . . . xii + 684 pp. + atlas of 14 + [2] pp. and 22 pls. Paris: De Boret.

DUMORTIER, B. C.

1822. Commentationes botanicae. 116 + [1] pp., 1 folding leaf. Tournay: Ch. Casterman-Dieu.

DUMORTIER, B. C. (Cont.)

1829. Analyse des familles des plantes, avec l'indication des principaux genres qui s'y rattachent. 104 pp. Tournay: J. Casterman.

EGEROD, LOIS E.

1952. An analysis of the siphonous Chlorophycophyta with special reference to the Siphonocladales, Siphonales and Dasycladales of Hawaii. Univ. Calif. Publ. Bot., 25:325–454, 23 figs., pls. 29–42.

EHRENBERG, D. C. G.

1832. Über die Entwickelung und Lebensdauer der Infusionsthiere; nebst ferneren Beiträgen zu einer Vergleichung ihrer organischen Systeme. Abh. K. Akad. Wiss. Berlin, 1831:1–154, 4 pls.

1836. Bemerkungen über feste mikroskopische, anorganische Formen in den erdigen und derben Mineralien. Ber. Verh. K. Preuss. Akad. Wiss. Berlin, 1836:84–85.

1838. Die Infusionsthierchen als vollkommene Organismen. Ein Blick in das tiefere organische Leben der Natur. xviii + [4] + 547 + [1] pp. and atlas of 64 pls. Leipzig: L. Voss.

1839. Über die Bildung der Kreidefelsen und des Kreidemergels durch unsichtbare Organismen. Abh. K. Akad. Wiss. Berlin, 1838:59–147, 3 charts, 4 pls.

1841. Über noch jetzt zahlreich lebende Thierarten der Kreidebildung und den Organismus der Polythalamien. Abh. K. Akad. Wiss. Berlin, 1939:81–174, 4 pls.

1853. Neuerlich bei Berlin vorgekommenen neuen Formen des mikroskopischen Lebens. Monatsber. Berlin Akad. Wiss., 1853:183–194.

EICHLER, A. W.

1880. Syllabus der Vorlesungen über specielle und medicinisch-pharmaceutische Botanik. iv + 47 pp. Berlin: Gebr. Borntraeger.

ELENKIN, A. A.

1916. Note sur le genre *Nodularia* Mert., suivie de la recherche critique sur la famille Nodulariaceae mihi. Bull. Jardin Imp. Bot. Pierre le Grand, 16(2):333–344. (Not seen, cited from Elenkin, 1917, p. 163.)

1917. Mémoire sur la modification des principes de classification des Hormogoneae (Thur.) Kirchn. (tribu des Cyanophycées). Journ. Soc. Bot. Russie, 1(3–4): 147–165, 5 figs.

1933. Über die systematische Einteilung der Ordnung Chroococcales Geitler (1925). Akad. Nauk Bot. Inst. Trudy (Acta Inst. Bot. Acad. Sci. U.S.S.R.), ser. 2, Pl. Crypt., Fasc. 1:17–21. (In Russian with a German summary.)

1934. Sur les principes fondamentaux du système des Cyanophyceae. Soviet Bot., 1934(5):51–83. (In Russian.)

1936. Monographia algarum cyanophycearum aquidulcium et terrestrium in finibus URSS inventarum. Vol. 1. 675 pp. Moscow, Leningrad. (Not seen, cited from Geitler, 1942.)

1938. Monographia algarum cyanophycearum aquidulcium et terrestrium in finibus URSS inventarum. Pars specialis (systematica) . . . Fasc. I . . . 984 pp., 290 figs. Moscow, Leningrad: Acad. Nauk.

1949. Monographia algarum cyanophycearum aquidulcium et terrestrium in finibus URSS inventarum. Pars specialis (systematica). Fasc. II . . . Pp. 985–1908, figs. 291–566, portr. Moscow, Leningrad: Acad. Nauk.

ELLIS, J.

1767. Sequel [to] extract of a letter from John Ellis, Esquire, F.R.S. to Dr. Linnaeus, of Upsal[a], F.R.S. on the animal nature of the genus of zoophytes, called *Corallina*. Philos. Trans. [Roy. Soc. London], 57:421–427, pl. 18.

ENDLICHER, S. L.

1836–1840. Genera plantarum secundum ordines naturales disposita. lx + 1483 pp. Vienna: Beck.

1843. Mantissa botanica altera. Sistens generum plantarum, suppl. 3. [6] + 111 pp. Vienna: Beck.

ENGLER, A.

1892. Syllabus der Vorlesungen über specialle und medicinisch-pharmaceutische Botanik. Eine Uebersicht über das gesammte Pflanzensystem mit Berücksichtigung der Medicinae- und Nutzpflanzen. Grosse Ausg. xxiii + 184 pp. Berlin: Gebr. Borntraeger.

1897. Bemerkung, betreffend der in der Abteilung I. 2 noch nicht berücksichtigten Chlorophyceae und Phaeophyceae. *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . Teil 1, Abt. 2, p. 570. Leipzig: W. Engelmann.

1898. Syllabus der Pflanzenfamilien . . . 2nd ed. xii + 214 pp. Berlin: Gebr. Borntraeger.

1903. Syllabus der Pflanzenfamilien . . . 3rd ed. xxvii + 233 pp. Berlin: Gebr. Borntraeger.

ENGLER, A., and E. GILG

1924. Syllabus der Pflanzenfamilien . . . 9th and 10th eds. xliii + 420 pp. Berlin: Gebr. Borntraeger.

ERCEGOVIĆ, A.

1932. Ekološke i sociološke studije o litofitskim cijanoficejama sa jugoslavenske obale Jadrana. Rad Jugoslav. Akad. Znanosti Umjetnosti, 244:129–220, 10 figs., 11 tables, 7 pls.

1949. Sur la *Yadranella*, nouveau genre d'algues de l'Adriatique et sur son développement. Acta Adriatica Inst. Oceanogr. Ribarstvo Split, 4(2):27–39, 4 figs.

ESPER, E. J. C.

1797–1808. Icones fucorum . . . 217 + 53 + 53bis–132 +iv + iii pp., pls. 1–29, 29A, 30–136, 136A, 137–144, 144A, 145–160, 160A, 161, 161A, 162, 162A, 163, 163A, 164–169, I–IV, I–IV. Nürnberg: Raspeschen Buchhandlung.

FALKENBERG, P.

1879. Die Befruchtung und der Generationswechsel von *Cutleria*. Mitt. Zool. Stat. Neapel, 1:420–447, pl. 13.

1882. Die Algen in weitesten Sinne. *In* A. Schenk, Handbuch der Botanik. Pp. 159–314, 25 figs. Breslau: Eduard Trewendt.

FARMER, J. B., and J. L. WILIAMS

1896. On fertilization and the segmentation of the spore in *Fucus*. Ann. Bot., 10: 479–487.

1898. Contributions to our knowledge of the Fucaceae: their life-history and cytology. Philos. Trans. Roy. Soc. London, ser. B, 190:623–645, pls. 19–24.

FELDMANN, J.

1937. Les algues marines de la côte des Albères. I–III. Cyanophycées, Chlorophycées, Phéophycées. Rev. Alg., 9(3–4): 141–335, 67 figs., 10 pls.

1938. Sur la classification de l'ordre des Siphonocladales. Rev. Gén. Bot., 50:571–597, 5 figs.

1946. Sur l'hétéroplastie de certaines Siphonales et leur classification. Compt. Rend. Acad. Sci. [Paris], 222:752–753.

1949. L'ordre des Scytosiphonales. Mém. Hist. Nat. Afr. Nord, hors-sér., 2:103–115, 3 figs.

FELDMANN, J. (Cont.)

1950. Sur l'existence d'une alternance de générations entre l'*Halicystis parvula* Schmitz et le *Derbesia tenuissima* (De Not.) Crn. Compt. Rend. Acad. Sci. [Paris], 230:322–323.

1952. Les cycles de reproduction des algues et leur rapports avec la phylogénie. Rev. Cytol. Biol. Vég., 13:1–49.

FORTI, A.

1907. Myxophyceae. *In* J. B. De Toni, Sylloge algarum . . . Vol. 5 [6] + 761 pp. Padua: Publ. by De Toni.

FOSLIE, M.

1890. Contributions to knowledge of the marine algae of Norway. I. East-Finmarken. Tromsø Mus. Aarshefter, 13:1–186, pls. 1–3.

FØYN, BIRGITHE R.

1934. Über den Lebenscyklus einiger Braunalgen. Vorläufige Mitteilung. Bergens Mus. Årbok, 1934:1–9.

FØYN, BJORN

1929. Untersuchungen über die Sexualität und Entwicklung von Algen. IV. Vorläufige Mitteilung über die Sexualität und den Generationswechsel von *Cladophora* und *Ulva*. Ber. Deutsch. Bot. Ges., 47:495–506, 2 figs., 2 tables.

1934a. Lebenszyklus, Cytologie und Sexualität der Chlorophycee *Cladophora Suhriana* Kützing. Archiv Protistenk., 83:1–56, 18 figs., 13 tables, pls. 1–5.

1934b. Lebenszyklus und Sexualität der Chlorophycee *Ulva lactuca* L. Archiv Protistenk., 83:154–177, 13 figs., 8 tables.

FRÉMY, P.

1930. Les myxophycées de l'Afrique equatoriale française. Arch. Bot., 3 (Mém. 2). 508 pp., 362 figs., 1 folding map.

1933. Cyanophycées des cotes d'Europe. Mém. Soc. Natl. Sci. Nat. et Math. Cherbourg, 41:1–235, pls. 1–66.

FRITSCH, F. E.

1929. The genus *Sphaeroplea*. Ann. Bot., 43:1–26, 8 figs.

1935. The Structure and Reproduction of the Algae, Vol. 1. xvii + 791 pp., 245 figs., frontis. Cambridge Univ. Press.

1939. The heterotrichous habit. Bot. Not., 1939:125–133.

1942. The interrelations and classification of the Myxophyceae (Cyanophyceae). New Phytol., 41:134–148, 5 figs.

1943. Studies in the comparative morphology of the algae III. Evolutionary tendencies and affinities among Phaeophyceae. Ann. Bot., n.s., 7:63–87, 4 figs.

1944. Present-day classification of algae. Bot. Rev., 10:233–277.

1945. The Structure and Reproduction of the Algae. Vol. 2. xiv + 939 pp., 336 figs., 2 maps, frontis. Cambridge Univ. Press.

1947. The status of the Siphonocladales. Journ. Indian Bot. Soc., M.O.P. Iyengar Commemoration Volume, pp. 29–50, 5 figs.

1951. The heterocyst: A botanical enigma. Proc. Linn. Soc. London, 162(2):194–211, 122 figs., pl. 5.

FUJIYAMA, T.

1949. On the asexual reproduction and life-history of *Prasiola* (Ag.) Menegh. in Japan. Bot. Mag. Tokyo, 62:57–61, 10 figs.

FUNK, G.

1927. Die Algenvegetation des Golfs von Neapel . . . Publ. Staz. Zool. Napoli, 7 (suppl.). 507 pp., 50 figs., 20 pls.

GEITLER, L.

1925a. Synoptische Darstellung der Cyanophyceen in morphologischer und systematischer Hinsicht. Beih. Bot. Cent., 41(3):163–294, pls. 17–20.

1925b. Cyanophyceae. *In* A. Pascher, Die Süsswasser-Flora Deutschlands, össterreichs und der Schweiz. Heft 12. viii + 450 + 464–481 pp., 560 figs. Jena: G. Fischer.

1927a. Die Reduktionsteilung und Copulation von *Cymbella lanceolata*. Archiv Protistenk., 58:465–507, 14 figs., pls. 8, 9.

1927b. Somatische Teilung, Reduktionsteilung, Copulation und Parthenogenese bei *Cocconeis placentula*. Archiv Protistenk., 59:506–549, 29 figs., pls. 12–14.

1928. Copulation und Geschlechtsverteilung bei einer *Nitzschia*-Art. Archiv Protistenk., 61:419–442, 13 figs.

1930–1932. Cyanophyceae. *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, österreich und der Schweiz. 2nd ed. Bd. 14 (issued by R. Kolkwitz). vi + 1196 pp., 780 figs. Leipzig: Akad. Verlagsges.

1933. Diagnosen neuer Blaualgen von den Sunda-Inseln. Arch. Hydrobiol. Suppl., 12:622–634.

1935. *Trypanochloris*, eine neue grüne Alge in den Schalen von Landschnecken und ihre Begleitflora. Biol. Generalis, 11(2): 135–148, 5 figs., pls. 2, 3.

1942. Schizophyta: Klasse Schizophyceae. *In* A. Engler and K. Prantl, Die Natürlichen Pflanzenfamilien . . . 2nd ed. (cont. by H. Harms and J. Mattfeld). Bd. 1b. iv + 232 pp., 156 figs. Leipzig: W. Engelmann.

1943. Eine neue atmophytische Chrysophycee, *Ruttnera spectabilis*, nov. gen., nova spec. Internat. Rev. Ges. Hydrobiol. Hydrograph. 43(1–3): 100–109, 2 figs.

1952. Oogamie, Mitose, Meiose und metagama Teilung bei der zentrischen Diatomee *Cyclotella*. österr. Bot. Zeitschr., 99:506–520, 5 figs.

GEMEINHARDT, K.

1930. Silicoflagellatae. *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, österreich und der Schweiz. 2nd ed. Bd. 10, Abt. 2 (issued by R. Kolkwitz). Pp. 1–85, 69 figs., pl. 1. Leipzig: Akad. Verlagsges.

1931. Die Silicoflagellaten der Deutschen Südpolar-Expedition 1901–1903. *In* E. von Drygalski, Deutsche Südpolar-Expedition 1901–1903 im Auftrage des Reichsministeriums des Innern, Bd. 20, pp. 217–258, 1 fig., pls. 42, 43. Berlin and Leipzig: Walter De Gruyter and Co.

1938–1940. Oedogoniales. *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, österreich und der Schweiz. 2nd ed. Bd. 12, Abt. 4 (issued by R. Kolkwitz). xii + 453 pp., 539 figs. Leipzig: Akad. Verlagsges.

GMELIN, S. G.

1768. Historia fucorum. [10] + 239 + 6 pp., pls. 1A, 1B, 2A, 2B, 3–33. Leningrad: Acad. Sci.

1788. See Linnaeus, C. 1788.

GOEBEL, K.

1930. Die Deutung der Characeen-Antheridium. Ein Versuch. Flora, 124:491–498, 3 figs.

GOLDFUSS, G. A.

1820. Handbuch der Zoologie. Vol. 1. xlvi + 696 pp., 2 pls. Nürnberg: Schrag.

GOMONT, M.

1892. Monographia des oscillariées (nostocacées homocystées). Ann. Sci. Nat. Bot., sér. 7, 15:263–368, pls. 6–14.

1893. Monographia des oscillariées (nostocacées homocystées) deuxième partie-lyngbyées. Ann. Sci. Nat. Bot., sér. 7, 16:91–264, pls. 1–7.

GOROSCHANKIN, J.

1891. Beiträge zur Kenntniss der Morphologie und Systematik der Chlamydomonaden. I. *Chlamydomonas Braunii* (Mihi). Bull. Soc. Imp. Nat. Moscou, n. s., 4:498–518, pls. 14, 15.

GRAHAM, H. W.

1951. Pyrrophyta. *In* G. M. Smith, ed., Manual of Phycology . . . Pp. 105–118, figs. 26–28. Waltham, Mass.: Chronica Botanica Co.

GRAY, S. F.

1821. A Natural Arrangement of British Plants, . . . Vol. 1. xxviii + 824 pp., 21 pls. London: Baldwin, Cradock, and Joy.

GREVILLE, R. K.

1830. Algae britannicae, . . . lxxxviii + 218 pp., 19 pls. Edinburgh: Maclachlan and Stewart.

GRIFFETH, J. W., and A. HENFREY

1856. The Micrographic Dictionary; a Guide to the Examination and Investigation of the Structure and Nature of Microscopic Objects. xl + 696 pp., 816 figs., 41 pls. London: van Voorst.

GROSS, F.

1934. Zur Biologie und Entwicklungsgeschichte von *Noctiluca miliaris*. Archiv Protistenk., 83:178–196, 6 figs., pl. 6.

GROVES, J., and G. R. BULLOCK-WEBSTER

1920. The British Charophyta. Vol. 1. xiv + 141 pp., pls. 1–20. London: Ray Society.

1924. The British Charophyta. Vol. 2. xi + 129 pp., pls. 21–45. London: Ray Society.

GRUNOW, A.

1860. Ueber neue oder ungenügend gekannte Algen. Verh. Zool.-Bot. Ges. Wien, 10: 503–582, pls. 3–7.

HAECKEL, E.

1862. Die Radiolarien. (Rhizopoda Radiaria.) Eine Monographie, Thiel 1. xiv + 572 pp. Berlin: G. Reimer.

1866. Generelle Morphologie der Organismen. Bd. 1. Allgemeine Anatomie der Organismen. xxxii + 574 pp., 2 pls. Berlin: G. Reimer.

1873. Natürliche Schöpfungsgeschichte. 4th ed. xlvi + 688 pp., 16 pls. Berlin: G. Reimer. (Not seen, cited from Kofoid, *in* Univ. Calif. Publ. Zool., 19:329, 1920.)

1894. Systematische Phylogenie der Protisten und Pflanzen. Theil 1. xv + 400 pp. Berlin: G. Reimer.

HAMEL, G.

1931–1939. Phéophycées de France. 1–80 + i–xlvii + 81–432 pp., 63 figs., 10 pls. Paris: Publ. by author.

HÄMMERLING, J.

1931. Entwicklung und Formbildungsvermögen von *Acetabularia mediterranea*. Biol. Zentralbl., 51:633–647, 6 figs., 1 table.

HANSGIRG, A.

1886. Prodromus der Algenflora von Böhmen, Theil 1, Heft 1. Archiv Naturwiss. Landesdurchforsch. Böhmen, 5, No. 6. 96 pp., 45 figs.

1888a. Prodromus der Algenflora von Böhmen, Theil 1, Heft 2. Archiv Naturwiss. Landesdurchforsch. Böhmen, 6, No. 6. 288 + [2] pp., figs. 46–124.

HANSGIRG, A. (Cont.)

1888b. Synopsis generum subgenerumque myxophycearum (cyanophycearum) hucusque cognitorum cum descriptione generis nov. "*Dactylococcopsis*." Notarisia, 3:548–590.

1892. Prodromus der Algenflora von Böhmen. Theil 2. Archiv Naturwiss. Landesdurchforsch. Böhmen, 8, No. 4. 268 pp., 68 figs.

HARTMANN, M.

1929. Untersuchungen über die Sexualität und Entwicklung von Algen. III. Über die Sexualität und den Generationswechsel von *Chaetomorpha* und *Enteromorpha*. Ber. Deutsch. Bot. Ges., 47:485–494, 1 fig., 2 tables.

HARVEY, W. H.

1836. Algae. *In* J. T. Mackay, Flora hibernica . . . , Pt. 3. Pp. 157–254. Dublin: William Curry and Co.

1841. A Manual of the British Algae . . . lvii + 229 pp. London: van Voorst.

1847. Nereis australis . . . viii + 124 pp., 50 pls. London: Reeve Bros.

1849. A Manual of the British Marine Algae . . . 2nd ed. lii + 252 pp., 27 pls. London: van Voorst.

1852. Nereis boreali-americana: . . . Pt. 1.—Melanospermeae. Smithson. Contr. Knowledge, 3 (Art. 4). 150 pp., pls. 1–12.

1853. Nereis boreali-americana: . . . Pt. 2.—Rhodospermeae. Smithson. Contr. Knowledge, 5 (Art. 5). 258 pp., pls. 13–36.

HASSALL, A. H.

1845. A History of the British Freshwater Algae . . . Vol. 1. viii + 462 + [1] pp. Vol. 2. 24 pp., 103 pls. London: Taylor, Walton, and Maberly. (Printing of 1852 and 1857 seen.)

HAUCK, F.

1883–1885. Die Meeresalgen Deutschlands und Oesterreichs. *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. 2nd ed. Bd. 2. xxiii + [1] + 575 pp., 236 figs., 5 pls. Leipzig: E. Kummer.

HEDWIG, J.

1798. Theoria generationis et fructificationis plantarum cryptogamicarum Linnaei retractata et aucta. x + 268 pp., pls. A, 1–42. Leipzig: Breitkopf.

HEERING, W.

1906. Die Süsswasseralgen Schleswig-Holsteins . . . 1. Teil: Einleitung.—Heterokontae. Mitt. Bot. Staatsinst. Hamburg, 1905:61–150, 43 figs.

1914. Chlorophyceae. III. Ulothricales, Microsporales, Oedogonales. *In* A. Pascher, Die Süsswasser-flora Deutschlands, österreichs und der Schweiz. Heft 6. iv + 250 pp., 384 figs. Jena: G. Fischer.

1921. Chlorophyceae IV. Siphonocladiales, Siphonales. *In* A. Pascher, Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz. Heft 7. iv + 103 pp., 94 figs. Jena: G. Fischer.

HERTWIG, O.

1876. Beiträge zur Kenntniss der Bildung, Befruchtung und Theilung des thierischen Eies. Morph. Jahrb., 1:347–434, pls. 10–13.

HIERONYMUS, G.

1905. Bemerkungen über *Chlamydomyxa labyrinthuloides* Archer und *Chlamydomyxa montana* Lankester. Hedwigia, 44:137–157.

HIRN, K. E.

1900. Monographie und Iconographie der Oedogoniaceen. Acta Soc. Sci. Fennicae, 27(1):i–iv, 1–394, [1], 64 pls.

HOFMEISTER, W.

1867. Die Lehre von der Pflanzenzelle. *In* Handbuch der physiologischen Botanik. Vol. 1(1). xii + 404 pp., 58 figs. Leipzig: W. Engelmann.

HOLLANDE, A.

1942. Étude cytologique et biologique de quelques flagellés libres. Volvocales, Cryptomonadines, Eugléniens, Protomastigines. Arch. Zool. Expériment. Gén., 83:1–268, 47 figs., pls. 1–17.

HOLLENBERG, G. J.

1940. New marine algae from southern California. I. Amer. Journ. Bot., 27:868–877, 17 figs.

HOVASSE, R.

1932. Contribution a l'étude des silicoflagellés . . . Bull. Biol. France et Belgique, 66:447–501, 11 figs., pls. 6, 7.

HUBER, J.

1892. Contributions a la connaissance des Chaetophorées épiphytes et endophytes et leur affinités Ann. Sci. Nat. Bot., sér. 7, 16:265–359, pls. 8–18.

HUBER-PESTALOZZI, G.

1938. Das Phytoplankton des Süsswassers . . . *In* A. Thienemann, Die Binnengewässer . . . Bd. 16, Teil 1. [5] + 342 pp., 395 figs. in text and on pls. 1–66. Stuttgart: Schweizerbart'sche Verlagsbuchhandlung.

1941. Die Phytoplankton des Süsswassers. Systematik und Biologie. *In* A. Thienemann, Die Binnengewässer . . . Bd. 16, Teil 2(1). [1] + 365 pp., 443 figs. Stuttgart: Schweizerbart'sche Verlagsbuchhandlung.

1950. Das Phytoplankton des Süsswassers . . . Teil 3, Cryptophyceen, Chloromonadinen, Peridineen. *In* A. Thienemann, Die Binnengewässer . . . Bd. 16, Teil 3. ix + 310 pp., 300 figs. Stuttgart: Schweizerbart'sche Verlagsbuchhandlung.

HUSTEDT, F.

1930. Bacillariophyta (Diatomeae). *In* A. Pascher, Die Süsswasser-Flora Mitteleuropas. 2nd ed. Heft. 10. viii + 466 pp., 875 figs. Jena: G. Fischer.

HUXLEY, T. H.

1858. Appendix A. Report on the examination of specimens of bottom. *In* J. Dayman, Deep-Sea Soundings in the North Atlantic Ocean between Ireland and Newfoundland, Made in H.M.S. "Cyclops" . . . 1857. London: Great Britain and Ireland.—Admiralty. (Not seen.)

HY, F.

1913. Les Characées de France. Soc. Bot. France, Mém. 26. 47 pp., 3 pls.

HYGEN, G.

1934. Über den Lebenszyklus und die Entwicklungsgeschichte der Phaeosporeen. Versuche an *Nemacystis divaricatus* (Ag.) Kuck. Nyt. Mag. Naturvidensk., 74:187–268, 11 figs., 16 pls.

ISHIKAWA, M.

1921. Cytological studies on *Porphyra tenera* Kjellm. I. Bot. Mag. Tokyo, 35:206–218, 14 figs., pl. 4.

1924. On the phylogeny of Rhodophyceae. Bot. Mag. Tokyo, 38:159–167. (In Japanese with an English summary on p. 130.)

IYENGAR, M.O.P.

1936. *Characiosiphon*, a new member of the Chlorophyceae. (Preliminary note.) Journ. Indian Bot. Soc., 15:313–318, 10 figs., pl. 23.

IYENGAR, M.O.P., and T. V. DESIKACHARY

1946. *Mastigocladopsis jogensis* gen. et. sp. nov., a new member of the Stigonemataceae. Proc. Indian Acad. Sci., 24:55–59, 13 figs., pl. 1.

IYENGAR, M.O.P., and K. R. RAMANATHAN

1940. On the reproduction of *Anadyomene stellata* (Wulf.) Ag. (Preliminary note.) Journ. Indian Bot. Soc., 19:175–176.

1941. On the life-history and cytology of *Microdictyon tenuius* (Ag.) Decsne. (Preliminary note.) Journ. Indian Bot. Soc., 20:157–159, 9 figs., pl. 3.

IYENGAR, M.O.P., and R. SUBRAHMANYAN

1942. On reduction division and auxosporeformation in *Cyclotella Meneghiniana* Kütz. (Preliminary note.) Journ. Indian Bot. Soc., 21:231–237, 14 figs., pl. 10.

1944. On reduction division and auxosporeformation in *Cyclotella Meneghiniana* Kütz. Journ. Indian Bot. Soc., 23:125–152, 63 figs., pls. 8, 9.

JAHN, T. L.

1946. The euglenoid flagellates. Quart. Rev. Biol., 21:246–274, 6 figs.

1951. Euglenophyta. *In* G. M. Smith, ed., Manual of Phycology. Pp. 69–81, figs. 18–20. Waltham, Mass.: Chronica Botanica Co.

JANCZEWSKI, E.

1876. Notes sur le développment du cystocarpe dans les Floridées. Mém. Soc. Natl. Sci. Nat. Cherbourg, 20:109–144, pls. 3–5.

JANE, F. W.

1946. A revision of the genus *Harpochytrium*. Jour. Linn. Soc. London, Bot., 53: 28–40, 28 figs.

JAO, C. C.

1941. Studies on the freshwater algae of China. IX. Coelodiscaceae, a new family of the Chlorophyceae. Sinensia, 12:291–298, pl. 1.

1947. *Coelodiscus bullatus*, sp. nov., a second species of the Coelodiscaceae. Bot. Bull. Acad. Sinica, 1:255–256, 1 fig.

JOHNSON, T.

1894. The systematic position of the Bangiaceae. Nuova Not., 5:636–647.

JORDE, I.

1933. Untersuschungen über den Lebenszyklus von *Urospora* Aresch. und *Codiolum* A. Braun. Nyt. Mag. Naturvidenskab., 73:1–19, 5 figs., pl. 1.

JULLER, E.

1937. Der Generations- und Phasenwechsel bei *Stigeoclonium subspinosum*. Archiv Protistenk., 89:55–93, 21 figs.

JUSSIEU, A. L. DE

1789. Genera plantarum . . . (24) + lxxii + 498 + [1] pp. Paris: Herissant.

KAMPTNER, E.

1928. Über das System und die Phylogenie der Kalkflagellaten. Archiv Protistenk., 64:19–43, 1 diagram.

KARSTEN, G.

1899. Die Diatomeen der Kieler Bucht. Wiss. Meeresuntersuch. Abt. Kiel, N.F., 4:17–205, 219 figs.

1912. Über die Reduktionsteilung bei der Auxosporenbildung von *Surirella saxonica*. Zeitschr. Bot., 4:417–426, pl. 7.

KARSTEN, G. (Cont.)

1928. Abteilung Bacillariophyta (Diatomeae). *In* A. Engler, Die natürlichen Pflanzenfamilien . . . 2nd ed. Bd. 2. pp. 105–303, figs. 93–424. Leipzig: W. Engelmann.

KAULFUSS, G. F.

1825. Erfahrungen über das Keimen der Charen, nebst andern Beiträgen zur Kenntniss dieser Pflanzengattung. [8] + 92 pp., 1 pl. Leipzig: Publ. by author?

KENT, W. S.

1880–1881. A Manual of the Infusoria: . . . Vol. 1. x + 472 pp. London: David Bogue.

KIRCHNER, O.

1878. Algen. *In* F. Cohn, Kryptogamen-Flora von Schlesien. Bd. 2(1). iv + [3] + 284 pp. Breslau: J. U. Kern's Verlag.

1898. Schizophyceae (Myxophyceae Stizenberger; Phycochromophyceae Rabenhorst; Cyanophyceae Sachs). *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . Teil I, Abt. 1a. Pp. 45–92, figs. 48–62. Leipzig: W. Engelmann.

KJELLMAN, F. R.

1880. Rhodospermeae et Fucoideae. *In* Enumerator plantae scandinaviae. Lund. (Not seen, cited from Kjellman, 1883.)

1883. The algae of the Arctic Sea. K. Svensk. Vet.-Akad. Handl., Vol. 20 (5). 350 + [1] pp., 5 tables, 31 pls.

1890. Handbok i skandinaviens hafsalgflora. [4] + 103 pp., 17 figs. Stockholm: O. L. Lamm.

1891–1893. Phaeophyceae. *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . Teil 1, Abt. 2. Pp. 176–290, figs. 129–188. Leipzig: W. Engelmann.

1893. Dictyotales. *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . Teil 1, Abt. 2. Pp. 291–297, figs. 189–191. Leipzig: W. Engelmann.

KLEBAHN, H.

1888. Ueber die Zygosporen einiger Conjugaten. Ber. Deutsch. Bot. Ges. 6:160–166, pl. 7.

1891. Studien über Zygoten I. Die Keimung von *Closterium* und *Cosmarium*. Jahrb. Wiss. Bot., 22:415–443, pls. 13, 14.

1892. Studien über Zygoten II. Die Befruchtung von *Oedogonium Boscii*. Jahrb. Wiss. Bot., 24:235–267, pl. 3.

1896. Beiträge zur Kenntniss der Auxosporenbildung. I. *Rhopalodia gibba* (Ehrenb.) O. Müller. Jahrb. Wiss. Bot., 29:595–654, pl. 10.

KLEBS, G.

1883. Über die Organisation einiger Flagellaten-Gruppen und ihre Beziehung zu Algen und Infusorien. Untersuch. Bot. Inst. Tübingen, 1(2):233–362, pls. 2, 3.

1884. Ein kleiner Beitrag zur Kenntniss der Peridineen. Bot. Zeit., 42:721–733, 737–745, pl. 10.

1892. Flagellatenstudien. I, II. Zeitschr. Wiss. Zool., 55:265–445, pls. 13–18.

1912. Über Flagellaten- und Algen-ähnliche Peridineen. Verh. Naturhist.-Medizin. Ver. Heidelberg, N. F., 11:369–451, 15 figs., pl. 10.

KNEBEL, G.

1935. Monographie der Algenreihe der Prasiolales, insbesondere von *Prasiola crispa*. Hedwigia, 75:1–120, 32 figs., 14 tables, 3 maps.

KNIEP, H.

1928. Die Sexualität der niederen Pflanzen . . . vi + 544 pp., 221 figs., 23 tables. Jena: G. Fischer.

KNIGHT, MARGERY

1923. Studies in the Ectocarpaceae. I. The life-history and cytology of *Pylaiella litoralis* Kjellm. Trans. Roy. Soc. Edinburgh, 53(17):343–360, 6 pls.

1929. Studies in the Ectocarpaceae. II. The life-history and cytology of *Ectocarpus siliculosus*, Dillw. Trans. Roy. Soc. Edinburgh, 56(15): 307–332, 3 figs., 6 pls.

1947. John Lloyd Williams [Obituary]. Proc. Linn. Soc. London, 158:72–74.

KOCH, W. J.

1951. A study of the motile cells of *Vaucheria*. Journ. Elisha Mitchell Sci. Soc., 67: 123–131, pls. 3–5.

KOFOID, C. A., and T. SKOGSBERG

1928. The Dinoflagellata: the Dinophysoidae. *In* Reports on the Scientific Results of the Expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross," . . . xxxv. Mem. Mus. Comp. Zool., Harvard College, Vol. 51. 766 pp., 103 figs., 31 pls.

KOFOID, C. A., and OLIVE SWEZY

1921. The Free-Living Unarmored Dinoflagellata. Mem. Univ. Calif., Vol. 5. viii + 562 pp., 388 figs., 12 pls.

KOLBE, R. W.

1948. Elektronenmikroskopische Untersuchungen von Diatomeenmembranen. Arkiv Bot. Vol. 33(17). 21 pp., 5 figs., 10 pls.

KOLKWITZ, R., and H. KRIEGER

1941–1944. Zygnemales. *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz. 2nd ed. Bd. 13, Abt. 2 (issued by R. Kolkwitz). [1] + 499 pp., figs. A-Z, 1–779, 4–9. Leipzig: Akad. Verlagsges.

KORNMANN, P.

1938. Zur Entwicklungsgeschichte von *Derbesia* und *Halicystis*. Planta, 28:464–470, 4 figs.

1953. Der Formenkreis von *Acinetospora crinita* (Carm.) nov. comb. Helgoländer Wiss. Meeresuntersuch., 4:205–224, 14 figs.

KORSCHIKOV, A. A.

1923. Über zwei neue Organismen aus der Gruppe der Volvocales. Russ. Arkhiv Protistol., 2:177–178, pl. 7.

1926. On some new organisms from the groups Volvocales and Protococcales, and on the genetic relations of these groups. Archiv Protistenk., 55:439–503, 14 figs., pls. 4–12.

1929. Studies on the chrysomonads. I. Archiv Protistenk., 67:253–290, pls. 8–11.

1930. On the origin of the diatoms. Beih. Bot. Centr. 46(Abt. 1, Heft 3):460–469, 1 fig.

1938. Volvocineae. (Not seen, cited from H. Skuja, 1939b.)

KOSSINSKAJA, K. K.

1926. De novo cyanophycearum genere *Tildenia* mihi ad novam familiam Tildeniaceae mihi ducto. Not. Syst. Inst. Crypt. Horti Bot. Principalis U.S.S.R., 4:76–88, pl. 2. (In Russian with a Latin résumé.)

KRIEGER, W.

1933–1937. Die Desmidiaceen Europas mit Berücksichtigung der aussereuropäischen Arten. *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz. 2nd ed. Bd. 13, Abt. 1 (issued by R. Kolkwitz). vi + 712 pp., 33 figs., 96 pls. Leipzig: Akad. Verlagsges.

1939. Die Desmidiaceen Europas mit Berücksichtigung der aussereuropäischen Arten. In *L.* Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich

KRIEGER, W. (Cont.)
und der Schweiz. 2nd ed. Bd. 13, Abt. 1, Teil 2 (issued by R. Kolkwitz). 117 pp., 1 fig., pls. 97–142. Leipzig: Akad. Verlagsges.

KUCKUCK, P.
1891. Beiträge zur Kenntniss der *Ectocarpus*-Arter der Kieler Föhrde. Bot. Centr., 48:1–6, 33–41, 65–71, 97–104, 129–141, 6 figs.
1929. Fragmente einer Monographie der Phaeosporeen. Wiss. Meeresuntersuch., Abt. Helgoland, N. F., 17(4). 93 pp., 155 figs. (W. Nienberg, ed.)

KUNIEDA, H.
1934. On the life-history of *Monostroma*. Proc. Imp. Acad. Tokyo, 10:103–106, 12 figs.

KURSSANOV, L. J., and N. M. SCHEMAKHANOVA
1927. Sur la succession des phases nucléaires chez les algues vertes. Le cycle de développement du *Chlorochytrium Lemnae* Cohn. Russ. Arkhiv Protistol., 6:131–146, pls. 9, 10.

KÜTZING, F. T.
1833a. Beitrag zur Kenntniss über die Entstehung und Metamorphose der niedern vegetabilischen Organismen, nebst einer systematischen Zusammenstellung der hierher gehörigen niedern Algenformen. Linnaea, 8:335–384, pls. 6–8.
1833b. Synopsis diatomearum oder Versuch einer systematischen Zusammenstellung der Diatomeen. Linnaea, 8:529–620, pls. 13–19.
1843. Phycologia generalis . . . xvi + 1–144 + xvii–xxxii + 145–458 + [1] pp., 80 pls. Leipzig: Brockhaus.
1844. Die kieselschaligen Bacillarien oder Diatomeen. [1]+ 152 pp., 30 pls. Nordhausen: Ferd. Förstemann. (Printing of 1865 seen.)
1845. Phycologia germanica . . . x + [1] + 340 pp. Nordhausen: Publ. by author.
1849. Species algarum vi + 922 pp. Leipzig: Brockhaus.

KYLIN, H.
1916. Über die Befruchtung und Reduktionsteilung bei *Nemalion multifidum*. Ber. Deutsch. Bot. Ges., 34(4):257–271, 7 figs.
1917. Über die Entwicklungsgeschichte und die systematische Stellung der Tilopterideen. Ber. Deutsch. Bot. Ges., 35:298–310.
1918. Studien über die Entwicklungsgeschichte der Phaeophyceen. Svensk Bot. Tidskr., 12:1–64, 30 figs.
1923. Studien über die Entwicklungsgeschichte der Florideen. K. Svensk. Vet.-Akad. Handl., 63(11). 139 pp., 82 figs.
1925. The marine red algae in the vicinity of the Biological Station at Friday Harbor, Wash. Lunds Univ. Årsskr., N. F., Avd. 2, 21(9). 87 pp., 47 figs.
1928. Entwicklungsgeschichtliche Florideenstudien. Lunds Univ. Årsskr., N. F., Avd. 2, 24(4). 127 pp., 64 figs.
1930a. Über die Entwicklungsgeschichte der Florideen. Lunds Univ. Årsskr., N. F., Avd. 2, 26(6). 104 pp., 56 figs.
1930b. Some physiological remarks on the relationship of the Bangiales. Bot. Not., 1930:417–420.
1932. Die Florideenordnung Gigartinales. Lunds Univ. Årsskr., N. F., Avd. 2, 28(8). 88 pp., 22 figs., 28 pls.
1933. Über die Entwicklungsgeschichte der Phaeophyceen. Lunds Univ. Årsskr., N. F., Avd. 2, 29(7). 102 pp., 35 figs., 2 pls.
1935. Über einige kalkbohrende Chlorophyceen. K. Fysiogr. Sällskap. Lund. Förhandl., 5(19). 19 pp., 7 figs.
1937a. Anatomie der Rhodophyceen. *In* K. Linsbauer, Handbuch der Pflanzenanatomie. Bd. 6, Teilband 2: Algen (B, g). viii + 347 pp., 252 figs. Berlin: Gebr. Borntraeger.

KYLIN, H. (Cont.)

1937b. Über eine marine *Porphyridium*-Art. K. Fysiogr. Sällskap. Lund. Förhandl., 7(10). 5 pp., 1 fig.

1937c. Bemerkungen über die Entwicklungsgeschichte einiger Phaeophyceen. Lunds Univ. Årsskr., N. F., Avd. 2, 33(1). 34 pp., 5 figs.

1938. Beziehungen zwischen Generationswechsel und Phylogenie. Archiv Protistenk., 90:432–447.

1940a. Die Phaeophyceenordnung Chordariales. Lunds Univ. Årsskr., N. F., Avd. 2, 36(9):67 pp., 30 figs., 8 pls.

1940b. Zur Entwicklungsgeschichte der Ordnung Fucales. Svensk Bot. Tidskr., 34: 301–314, 1 fig.

1943a. Zur Biochemie der Cyanophyceen. K. Fysiogr. Sällskap. Lund Förhandl., 13(7). 14 pp.

1943b. Verwandtschaftliche Beziehungen zwischen den Cyanophyceen und den Rhodophyceen. K. Fysiogr. Sällskap. Lund Förhandl., 13(17). 7 pp.

1944a. Die Rhodophyceen der schwedischen Westküste. Lunds Univ. Årsskr., N. F., Avd. 2, 40(2). 104 pp., 53 figs., 32 pls.

1944. Über die Auxiliarzellen der Florideen. K. Fysiogr. Sällskap. Lund Förhandl., 14(20). 11 pp., 4 figs.

1947. Die Phaeophyceen der schwedischen Westküste. Lunds Univ. Årsskr., N. F., Avd. 2, 43(4). 99 pp., 61 figs., 18 pls.

LACKEY, J. B.

1939. Notes on plankton flagellates from the Scioto River (with description of new forms). Lloydia, 2:128–143, 38 figs.

LAMARCK, J. B. DE, and A. P. DE CANDOLLE

1805. Flore française . . . 3rd ed. Vol. 2 xli + 600 pp., map. Paris: Desray.

LAMOUROUX, J. V. F.

1805. Dissertations sur plusieurs espèces de *Fucus*, peu connues ou nouvelles, avec leur description en Latin et en Français. xxiv + 83 + [1] pp., 36 pls. Agen: Noubel.

1813. Essai sur les genres de la famille des thalassiophytes non articulées. Ann. Mus. Hist. Nat. [Paris], 20:21–47, 115–139, 267–293, pls. 7–13.

LE JOLIS, A.

1863. Liste des algues marines de Cherbourg. 168 pp., 6 pls. Paris: Baillière et Fils. (1880 printing seen.) (Also publ. in Mém. Soc. Imp. Sci. Nat. Cherbourg 10, 1864.)

LEMMERMANN, E.

1899. Planktonalgen. *In* H. Schauinsland, Ergebnisse einer Reise nach dem Pacific. Abhl. Nat. Ver. Bremen, 16(2):313–398, pls. 1–3.

1901a. Beiträge zur Kenntniss der Planktonalgen. Ber. Deutsch. Bot. Ges. 19:85–95, pl. 4.

1901b. Silicoflagellatae. Ergebnisse einer Riese nach dem Pacific.–H. Schauinsland 1896/97. Ber. Deutsch. Bot. Ges., 19:247–271, pls. 10, 11.

1907–1910. Algen I (Schizophyceen, Flagellaten, Peridineen). *In* Kryptogamenflora der Mark Brandenburg und angrenzender Gebiete herausgegeben von dem Botanischen Verein der Provinz Brandenburg. Bd. 3. x + (1)–(29) + 712 pp., 816 figs. Leipzig: Gebr. Borntraeger.

1908. Flagellatae, Chlorophyceae, Coccosphaerales und Silicoflagellatae. *In* K. Brandt and C. Apstein, Nordisches Plankton, Botanischer Teil, 21. 40 pp., 135 figs. Kiel and Leipzig: Lipsius and Tischer.

LEMMERMANN, E. (Cont.)

1913. Eugleninae. *In* A. Pascher, Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz. Heft. 2: Flagellatae II. Pp. 115–174, figs. 181–378. Jena: G. Fischer.

1914. Pantostomatinae, Protomastiginae, Distomatinae. *In* A. Pascher, Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz. Heft 1: Flagellatae I. Pp. 28–138. Jena: G. Fischer.

1915. Tetrasporales. *In* A. Pascher, Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz. Heft. 5: Chlorophyceae II. Pp. 21–51, 33 figs. Jena: G. Fischer.

LEVRING, T.

1941. Die Meeresalgen der Juan Fernandez-Inseln. *In* C. Skottsberg, The Natural History of Juan Fernandez and Easter Island. Vol. 2. Pp. 601–670, 30 figs., pls. 49–53.

LEWIS, I. F.

1909. The life history of *Griffithsia Bornetiana*. Ann. Bot., 23:639–690, 2 figs., pls. 49–53.

1912. Alternation of generations in certain Florideae. Bot. Gaz., 53:236–242.

LINDLEY, J.

1836. A Natural System of Botany;...2nd ed. xxvi + 526 pp. London: Longman, *et al.*

LINDEMANN, E.

1928. Peridineae (Dinoflagellatae). *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . 2nd ed. (issued by A. Engler) Bd. 2 (E. Jahn, ed.). Pp. 3–104, figs. 1–92. Leipzig: W. Engelmann.

LINDSTEDT, A.

1943. Die Flora der marinen Cyanophyceen der schwedischen Westküte. 121 + [1] pp., 2 figs., 3 tables, 11 pls. Thesis. Lund: Publ. by author.

LINNAEUS, C.

1753. Species plantarum . . . Vol. 2. Pp. 561–1200 + [31]. Stockholm: Salvius.

1788. Systema naturae . . . 13th ed. (J. F. Gmelin, ed.). Vol. 1(6). Pp. 3021–3909. Leipzig: G. E. Beer.

LOHMANN, H.

1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten, zugleich ein Beitrag zur Kenntnis des Mittelmeerauftriebs. Archiv Protistenk., 1:89–165, pls. 4–6.

1904. Eier und sogenannte Cysten der Plankton-Expedition. Ergebn. Plankton Exped. Humboldt-Stiftung. Vol. 4(N). 61 + [1] pp., 7 pls. Kiel and Leipzig: Lipsius and Tischer.

LONGEST, PAULINE M.

1946. Structure of the cilia in *Ectocarpus Mitchellae* and *Codium decorticatum*. Journ. Elisha Mitchell Sci. Soc., 62:249–252, 3 figs.

LUERSSEN, C.

1879. Handbuch der systematischen Botanik . . . Bd. 1. Kryptogamen. xii + 657 pp., 181 figs. Leipzig: Haessel.

LUTHER, A.

1899. Ueber *Chlorosaccus* eine neue Gattung der Süsswasseralgen, nebst einigen Bemerkungen zur Systematik verwandter Algen. Bihang K. Svensk. Vet.-Akad. Handl., 24, Afd. 3, No. 13. 22 pp., 1 folding pl.

LYNGBYE, H. C.

1819. Tentamen hydrophytologiae danicae . . . xxxii + 248 pp., 70 pls. Copenhagen: Schultz.

MACDONALD, J. D.

1869. On the structure of the diatomaceous frustule, and its genetic cycle. Ann. Mag. Nat. Hist., ser. 4, 3:1–8, pl. 3.

MACK, B.

1951. Morphologische und entwicklungsgeschichtliche Untersuchungen an Chrysophyceen. öster. Bot. Zeitschr., 98:249–279, 3 figs.

MANGENOT, G.

1948. Sur les caractères et la position systématique du genre *Phyllosiphon*. Compt. Rend. Acad. Sci. [Paris], 226:1103–1105.

MANTON, IRENE, and B. CLARKE

1951a. Electron microscope observations on the zoospores of *Pylaiella* and *Laminaria*. Journ. Exp. Bot., 2:242–246, 8 pls.

1951b. An electron microscope study of the spermatozoid of *Fucus serratus*. Ann. Bot., n. s., 15:461–471, pls. 20–24.

MANTON, IRENE, B. CLARKE, and A. D. GREENWOOD

1953. Further observations with the electron microscope on spermatozoids in the brown algae. Journ. Exp. Bot., 4:319–329, 2 figs., pls. 1–9.

MÄDLER, K.

1952. Charophyten aus dem Nordwestdeutschen Kimmeridge. Geol. Jahrb., 67:1–45, inc. pls. A, B, and 8 figs.

1953. Ein neues System der fossilen Charophyten. Flora, 140:474–484, 17 figs., pls. 2–5.

MARCHAND, L.

1895. Synopsis et tableau synoptique des familles qui composent la classe des Phycophytes (Algues, Diatomées et Bactériens). *In* Sous-règne des Cryptogames, 2e Embranchement. 20 pp., 1 chart. Paris: Soc. d'Edit. Sci.

MARTIN, MARGARET T.

1939. The structure and reproduction of *Chaetangium saccatum* (Lamour.) J. Ag.-II. Female plants. Journ. Linn. Soc. Bot., 52:115–144, 38 figs., pl. 1.

MERESCHKOWSKY, C.

1879. Studien über Protozoen des nördlichen Russland. Archiv Mikr. Anat., 16:153–248, pls. 10, 11.

MEYEN, J.

1827. Ueber die Priestleysche grüne Materie, wie über die Metamorphose des *Protococcus viridis* in *Priestleya botryoides* und in *Ulva terrestris*. Linnaea, 2: 388–409, pl. 7.

MEYER, K.

1929. Über die Auxosporenbildung bei *Gomphonema geminatum*. Archiv Protistenk., 66:421–435, pls. 15, 16.

MIGULA, W.

1890–1897. Die Characeen. *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. 2nd edit. Bd. 5. xv + 765 pp., 149 figs. Leipzig: E. Kummer. (For dates of parts see Groves and Bullock-Webster, 1924, p. 111.)

1895. Schizomycetes. *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . Teil 1, Abt. 1a. 44 pp., 47 figs. Leipzig: W. Engelmann.

1925. Charophyta-(Charales). *In* A. Pascher, Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz. Heft 11. Pp. 207–243, 14 figs. Jena: G. Fischer.

MITCHELL, MARGARET O., and FRANCES G. WHITTING

1892. On *Splachnidium rugosum*, Grev., the type of a new order of algae. *In* G. Murray, ed., Phycological Memoirs, Pt. 1. Pp. 1–10, pls. 1–3. London: Dulau and Co.

MÖBIUS, M.

1937. Geschichte der Botanik von den ersten Anfängen bis zur Gegenwart. vi + 458 pp. Jena: G. Fischer.

MOEWUS, F.

1940. Über die Sexualität von *Botrydium granulatum*. Biol. Zentralbl., 60:484–498, 2 figs., 6 tables.

MÜLLER, O.

1889. Durchbrechung der Zellwand in ihren Beziehungen zur Ortsbewegung der Bacillariaceen. Ber. Deutsch. Bot. Ges., 7:169–180, pl. 7.

1895. Ueber Achsen, Orientirungs- und Symmetrie-ebenen bei den Bacillariaceen. Ber. Deutsch. Bot. Ges., 13:222–234, pl. 20.

MÜLLER, O. F.

1773. Vermium terrestrium et fluviatilium, seu animalium infusoriorum, helminthicorum et testaceorum . . . Vol. 1, pt. 1. [32] + 135 pp. Copenhagen and Leipzig: Heineck and Faber.

1782. Icones plantarum sponte nascentium in regnis daniae et norvegiae . . . Vol. 5, fasc. 15. Pls. 841–900. Copenhagen: Möller.

1783. Strand-pärlebandet och armbandet, tvänne microscopiska strandväxter. K. Sv. Vet.-Akad. Handl., ser. 2, 4:80–85, pl. 3.

1786. Animalcula infusoria fluviatilia et marina . . . Opus hoc posthumum . . . cura O. Fabricii. [8] + lvi + 367 pp., 50 pls. Copenhagen: Möller.

MURRAY, G.

1895. An Introduction to the Study of Seaweeds. xvi + 271 pp., 88 figs., 8 pls. London: Macmillan and Co.

1897. On the reproduction of some marine diatoms. Proc. Roy. Soc. Edinburgh, 21: 207–219, pls. 1-3.

MURRAY, G., and V. H. BLACKMAN

1898. On the nature of the coccospheres and rhabdospheres. Philos. Trans. Roy. Soc. London, 190 (ser. B):427–441, pls. 15, 16.

MURRAY, J.

1891. Deep-sea deposits. Rept. Sci. Results Voyage H.M.S. "Challenger" 1873–76. Pp. 257–258, figs. 19–21. Edinburgh: Neill and Co.

NÄGELI, C.

1847. Die neuern Algensysteme und Versuch zur Begründung eines eigenen Systems der Algen und Florideen. Neue Denkschr. Allgemein. Schweiz. Ges. Gesammt. Naturwiss., 9 (unnumbered art. No. 2). 275 pp., 10 pls.

1849. Gattungen einzelliger Algen physiologisch und systematisch bearbeitet. Neue Denkschr. Allgemein. Schweiz. Ges. Gesammt. Naturwiss., 10 (Art. 7). viii + 139 pp., 8 pls.

1861. Beiträge zur Morphologie und Systematik der Ceramiaceae. Sitzungsber. K. Bayer. Akad. Wiss. München, 2:297–415, 1 pl.

NASR, A. H.

1947. Synopsis of the marine algae of the Egyptian Red Sea coast. Bull. Faculty Sci. Fouad I Univ. no. 26. 155 pp., 25 figs., 14 pls.

NEWTON, LINDA M.

1953. Marine algae. *In* The John Murray Expedition 1933–34 Scientific Reports. Vol. 9, No. 5. Pp. 395–420, pls. 1–4. London: British Museum (Natural History).

NITZSCH, C. L.

1817. Beitrag zur Infusorienkunde oder Naturbeschreibung der Zerkarien und Bazillarien. viii + 128 pp., 6 pls. Halle: J. C. Hendel.

OEHLKERS, F.

1916. Beitrag zur Kenntnis der Kernteilungen bei den Charazeen. Ber. Deutsch. Bot. Ges., 34(4):223–227, 1 fig.

OLTMANNS, F.

1889. Beiträge zur Kenntniss der Fucaceen. Bibl. Bot. Vol. 3(14). 100 pp., 15 pls.

1898. Zur Entwickelungsgeschichte der Florideen. Bot. Zeit., 56:99–140, 2 figs., pls. 4–7.

1899. Ueber die Sexualität der Ectocarpeen. Flora, 86:86–99, 16 figs.

1904. Morphologie und Biologie der Algen. Bd. 1. vi + 733 pp., 467 figs. Jena: G. Fischer.

1922a. Morphologie und Biologie der Algen. 2nd ed. Bd. 1. Chrysophyceae—Chlorophyceae. vi + 459 pp., 287 figs. Jena: G. Fischer.

1922b. Morphologie und Biologie der Algen. 2nd ed. Bd. 2. Phaeophyceae—Rhodophyceae. iv + 439 pp., figs. 288–612. Jena: G. Fischer.

OSTERHOUT, W. J. V.

1900. Befruchtung bei *Batrachospermum*. Flora, 87:109–115, pl. 5.

PALLA, E.

1894. Ueber eine neue, pyrenoidlose Art und Gattung der Conjugaten. Ber. Deutsch. Ges., 12:228–236, pl. 18.

PAPENFUSS, G. F.

1933. Notes on the life-cycle of *Ectocarpus siliculosus* Dillw. Science, 77:390–391.

1935. Alternation of generations in *Ectocarpus siliculosus*. Bot. Gaz., 96:421–446, 13 figs., pls. 6, 7.

1946. Proposed names for the phyla of algae. Bull. Torrey Club, 73:217–218.

1947. Extension of the brown algal order Dictyosiphonales to include the Punctariales. Bull. Torrey Club, 74:398–402.

1950a. Review of the genera of algae described by Stackhouse. Hydrobiologia, 2: 181–208.

1950b. Culturing of marine algae in relation to problems in morphology. *In* J. Brunel, G. W. Prescott, and L. H. Tiffany, eds., The Culturing of Algae, a Symposium. Pp. 77–95, 10 figs. The Charles F. Kettering Foundation.

1951a. Phaeophyta. *In* G. M. Smith, ed., Manual of Phycology . . . Pp. 119–158, figs. 29–37. Waltham, Mass.: Chronica Botanica Co.

1951b. Problems in the classification of the marine algae. Svensk Bot. Tidskr., 45: 4–11, 2 figs.

PASCHER, A.

1910. Chrysomonaden aus dem Hirschberger Grossteiche. Monogr. Abh. Intern. Rev. Gesammt. Hydrobiol. Hydrogr. Vol. 1. 66 pp., 3 pls.

1911a. *Cyrtophora*, eine neue tentakeltragende Chrysomonade aus Franzensbad und ihre Verwandten. Ber. Deutsch. Bot. Ges., 29:112–125, 3 figs., pl. 6.

1911b. Über die Beziehungen der Cryptomonaden zu den Algen. Ber. Deutsch. Bot. Ges., 29:193–203.

PASCHER, A. (Cont.)

1912a. Über Rhizopoden- und Palmellastadien bei Flagellaten (Chrysomonaden), nebst einer Übersicht über die braunen Flagellaten. Archiv Protistenk., 25: 153–200, 7 figs., 1 chart, pl. 9.

1912b. Zur Gliederung der Heterokonten. (Kleine Beiträge zur Kenntnis unserer Mikroflora 3.) Hedwigia, 53:6–22, 8 figs.

1913a. Chrysomonadinae. *In* Pascher, Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz. Heft 2: Flagellatae II. Pp. 7–95, figs. 1–150. Jena: G. Fischer.

1913b. Cryptomonadinae. *In* Pascher, Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz. Heft 2: Flagellatae II. Pp. 96–114, figs. 151–180. Jena: G. Fischer.

1913c. Chloromonadinae. *In* Pascher, Die Süsswasserflora Deutschlands, österreichs und der Schweiz. Heft 2: Flagellatae II. Pp. 175–181, figs. 379–387. Jena: G. Fischer.

1914. Über Flagellaten und Algen. Ber. Deutsch. Bot. Ges., 32:136–160.

1915. Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz. Heft 5: Chlorophyceae II, Einleitung. Pp. 1–20. Jena: G. Fischer.

1916a. Zur Auffassung der farblosen Flagellatenreihen. Ber. Deutsch. Bot. Ges., 34(7):440–447.

1916b. Über eine neue Amöbe—*Dinamoebe* (*varians*)—mit dinoflagellatenartigen Schwärmern. Archiv Protistenk., 36:118–136, 4 figs., pl. 10.

1917. Flagellaten und Rhizopoden in ihren gegenseitigen Beziehungen. Versuch einer Ableitung der Rhizopoden. Archiv Protistenk., 38:1–88, 65 figs.

1921. Über die Übereinstimmung zwischen den Diatomeen, Heterokonten und Chrysomonaden. Ber. Deutsch. Bot. Ges., 39:236–248, 6 figs.

1924. Zur Homologisierung der Chrysomonadencysten mit den Endosporen der Diatomeen. Archiv Protistenk., 48:196–203, 4 figs.

1925a. Heterokontae. *In* Pascher, Die Süsswasser-Flora Deutschlands, österreichs und der Schweiz. Heft 2. iv + 118 pp., 96 figs. Jena: G. Fischer.

1925b. Die braune Algenreihe der Chrysophyceen. Archiv Protistenk., 52:489–564, 56 figs., pl. 15.

1927a. Die braune Algenreihe aus der Verwandtschaft der Dinoflagellaten (Dinophyceen). Archiv Protistenk., 58:1–54, 38 figs.

1927b. Die Süsswasserflora Deutschlands, österreichs und der Schweiz. Heft 4. 506 pp., 451 figs. Jena: G. Fischer.

1929a. Beiträge zur allgemeinen Zellehre. I. Doppelzellige Flagellaten und Parallelentwicklungen zwischen Flagellaten und Algenschwärmern. Archiv Protistenk., 68:261–304, 21 figs.

1929b. Über die Teilungsvorgänge bei einer neuen Blaualge: *Endonema*. Jahrb. Wiss. Bot., 70:329–347, 10 figs.

1930a. Zur Kenntnis der heterokonten Algen. Archiv Protistenk., 69:401–451, 45 figs., pl. 21.

1930b. Zur Verwandtschaft der Monadaceae mit den Chrysomonaden: eine gehäusebewohnende, farblose Chrysomonade. Ann. Protistol., 2(4): 157–168, 6 figs.

1930c. Über einen grünen, assimilationsfähigen plasmodialen Organismus in den Blättern von *Sphagnum*. Archiv Protistenk., 72:311–358, 27 figs., pls. 20, 21.

1931. Systematische Übersicht über die mit Flagellaten in Zusammenhang steheden Algenreihen und Versuch einer Einreihung dieser Algenstämme in die Stämme des Pflanzenreiches. Beih. Bot. Centr., 48 (Abt. II):317–332.

1932. Über die Verbreitung endogener bzw. endoplasmatisch gebildeter Sporen bei den Algen. Beih. Bot. Centr., 49:293–308, 13 figs.

PASCHER, A. (Cont.)

1937–1939. Heterokonten. *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz. 2nd ed. Bd. 2 (issued by R. Kolkwitz). x + ii + 1092 pp., 912 figs. Leipzig: Akad. Verlagsges.

1939. Über gelegentliche Synzoosporenbildungen bei Algen und über die Verbreitung synzoosporer Organisationen. Beih. Bot. Centr., 59 (Abt. A):389–408, 20 figs.

1953. Lebenslauf und Arbeitenverzeichnis. Archiv Protistenk., 98:iii–xxxii.

PECK, R. E.

1934. The North American trochiliscids, Paleozoic Charophyta. Journ. Paleont., 8:83–119, 2 figs., pls. 9–13.

1946. Fossil Charophyta. Amer. Mid. Nat., 36:275–278, 6 figs.

PERSIDSKY, B. M.

1929. The development of the auxospores in the group of the Centricae (Bacillariaceae). 11 pp., 22 figs., 1 double pl. Moskow. (Not seen, cited from the review by P. Schmidt in Zeitschr. Bot., 22[9]:459–461, 1930.)

1935. The sexual process in *Melosira varians*. Beih. Bot. Centr., 53 (Abt. A):122–132, 23 figs.

PERTY, M.

1852. Zur Kenntniss kleinster Lebensformen nach Bau, Funktionen, Systematik, mit Specialverzeichniss der in der Schweiz beobachteten. viii + 228 pp., 17 pls. Bern: Jent and Reinert.

PETERSEN, J. B.

1918. Om *Synura Uvella* Stein og nogle andre Chrysomonadiner. Videnskab. Medd. Dansk Naturhist. Foren. Kjøbenhavn, 69:345–357, pl. 5.

1929. Beiträge zur Kenntnis der Flagellatengeisseln. Bot. Tidsskr. 40(5):373–389, 11 figs.

PFITZER, E.

1869. Ueber Bau und Zelltheilung die Diatomaceen. Sitzungsber. Niederrhein. Ges. Natur. Heilk. Bonn, 26:86–89.

1871. Untersuchungen über Bau und Entwicklung der Bacillariaceen (Diatomaceen). *In* J. Hanstein, Botanische Abhandlungen aus dem Gebiet der Morphologie und Physiologie. Heft 2. vi + 189 pp., 6 pls. Bonn: A. Marcus.

PIA, J.

1927. Thallophyta. *In* M. Hirmer, Handbuch der Paläobotanik. Bd. 1. Pp. 31–136, figs. 14–129. Munich and Berlin: Oldenbourg.

PITELKA, DOROTHY R.

1949. Observations on flagellum structure in Flagellata. Univ. Calif. Publ. Zool., 53(11):377–429, incl. pls. 37–46, 3 figs.

POCHE, F.

1913. Das System der Protozoa. Archiv Protistenk., 30:125–321, 1 fig.

POCOCK, MARY A.

1954. Two multicellular motile green algae, *Volvulina* Playfair and *Astrephomene*, a new genus. Trans. Roy. Soc. So. Afr., 34:103–127, 30 figs., pl. 2.

PRESCOTT, G. W.

1951. Algae of the Western Great Lakes Area Exclusive of Desmids and Diatoms. xiii + 946 pp., incl. 136 pls., text figs. 1–9, tables 1–7, 13 pp. (52–64) of unnumbered illus. Cranbrook Inst. Sci. Bull., No. 31.

PRINGSHEIM, E. G.

1944. Some aspects of taxonomy in the Cryptophyceae. New Phytol., 43:143–150.

1948a. Taxonomic problems in the Euglenineae. Biol. Rev., 23:46–61, 4 figs.

PRINGSHEIM, E. G. (Cont.)

1948b. The loss of chromatophores in *Euglena gracilis*. With a cytological contribution by R. Hovasse. New Phytol., 47:52–87, 13 figs.

1949. The relationship between bacteria and Myxophyceae. Bact. Rev., 13:47–98.

PRINGSHEIM, E. G. and OLGA

1952. Experimental elimination of chromatophores and eye-spot in *Euglena gracilis*. New Phytol., 51:65–76.

PRINGSHEIM, E. G., and R. HOVASSE

1950. Les relations de parenté entre Astasiacées et Euglènacées. Arch. Zool. Expér. Gén., 86(8):499–549, 14 figs., pl. 16.

PRINGSHEIM, N.

1855 Über die Befruchtung der Algen. Ber. Verh. K. Preuss. Akad. Wiss. Berlin, 1855:133–165, 1 folding pl.

1856. Über die Befruchtung und den Generationswechsel der Algen. Monatsber. K. Preuss. Akad. Wiss. Berlin, 1856:225–237, 1 pl.

1860. Beiträge zur Morphologie und Systematik der Algen. III. Die Coleochaeteen. Jahrb. Wiss. Bot. 2:1–38, pls. 1–6.

1863a. Über die Vorkeime der Charen. Monatsber. K. Preuss. Akad. Wiss. Berlin, 1862:225–231.

1863b. Ueber die Vorkeime und die nacktfüssigen Zweige der Charen. Jahrb. Wiss. Bot., 3:294–324, pls. 9–13.

1870. Über Paarung von Schwärmsporen, die morphologische Grundform der Zeugung im Pflanzenreiche. Monatsber. K. Preuss. Akad. Wiss. Berlin, 1869: 721–738, 1 folding pl.

PRINTZ, H.

1927. Chlorophyceae. *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . 2nd ed. Vol. 3. iv + 463 pp., 366 figs. Leipzig: W. Engelmann.

RABENHORST, L.

1847. Deutschlands Kryptogamen-Flora . . . Bd. 2, Abt. 2: Algen. xix + [1] + 216 pp. Leipzig: E. Kummer.

1853. Die Süsswasser-Diatomaceen. (Bacillarien.) Für Freude der Mikroskopie. xii + 72 pp., 10 pls. Leipzig: E. Kummer.

1863. Kryptogamen-Flora von Sachsen, der Ober-Lausitz, Thüringen und Nordböhmen . . . Abt. 1. xx + 653 pp., illustr. with text figs. Leipzig: E. Kummer.

1864. Flora europaea algarum aquae dulcis et submarinae. Sectio I. Algas diatomaceas complectens. 359 pp., illustr. with text figs. Leipzig: E. Kummer.

1865. Flora europaea algarum aquae dulcis et submarinae. Sectio II. Algas phycochromaceas complectens. 319 pp., illustr. with text figs. Leipzig: E. Kummer.

1868. Flora europaea algarum aquae dulcis et submarinae. Sectio III. Algas chlorophyllophyceas, melanophyceas et rhodophyceas complectens. xx + 461 pp., illustr. with text figs. Leipzig: E. Kummer.

RALFS, J.

1848. The British Desmidieae. xxii + 226 pp., 35 pls. London: Reeve, Benham, and Reeve.

REINKE, J.

1877. Über das Wachsthum und die Fortpflanzung von *Zanardinia collaris* Crouan. (*Z. prototypus* Nardo.) Monatsber. K. Preuss. Akad. Wiss. Berlin, 1876: 565–578, 1 pl.

1878. Entwicklungsgeschichtliche Untersuchungen über die Cutleriaceen des Golfs von Neapel. Nova Acta K. Leop.-Carol. Deutsch. Akad. Naturforsch., 40(2): 59–96, pls. 8–11.

ROSENBERG, MARIE

1930. Die geschlechtliche Fortpflanzung von *Botrydium granulatum* Grev. österr. Bot. Zeitschr., 79:289–296, 4 figs., 1 pl.

ROSENBERG, T.

1933. Studien über Rhodomelaceen und Dasyaceen. 87 pp., 25 figs. Thesis. Lund: Publ. by author.

ROSENVINGE, L. K.

1909. The marine algae of Denmark . . . Part 1. Introduction. Rhodophyceae I. (Bangiales and Nemalionales.) K. Dansk. Vidensk. Selsk. Skrifter, 7. Raekke, Naturvidensk. Math. Afd., 7(1). 151 pp., 73 figs., 2 maps, 2 pls.

ROSTAFINSKI, J.

1882. L'*Hydrurus* et ses affinités. Ann. Sci. Nat. Bot., ser. 6, 14:5–25, pl. 1.

ROSTAFINSKI, J., and M. WORONIN

1877. Ueber *Botrydium granulatum*. Bot. Zeit., 35:649–671, pls. 7–11.

RUPRECHT, F. J.

1851. Tange des Ochotskischen Meeres. *In* A. Th. v. Middendorff's Sibirische Reise, Botanik. Bd. 1(2). Pp. 191–435, pls. 9–18. Leningrad: K. Akad. Wiss.

1855. Über das System der Rhodophyceae. Mém. Acad. Imp. Sci. Saint-Pétersbourg, ser. 6, Sci. Nat. Bot., 7:25–54, 1 pl.

SACHS, J.

1874. Lehrbuch der Botanik . . . 4th ed. xvi + 928 pp., 492 figs. Leipzig: W. Engelmann.

1875. Textbook of botany . . . (1st Eng. ed., trans. and annotated by A. W. Bennett and W. T. T. Dyer.) xii + 858 pp., 461 figs. Oxford: Clarendon Press.

SAUVAGEAU, C.

1896a. Sur la conjugaison des zoospores de l'*Ectocarpus siliculosis*. Compt. Rend. Acad. Sci. [Paris], 123:431–433.

1896b. Remarques sur la reproduction des Phéosporées et en particulier des *Ectocarpus*. Ann. Sci. Nat. Bot., sér 8, 2:223–274.

1897. La copulation isogamique de l'*Ectocarpus siliculosus* est-elle apparente ou réele? Mém. Soc. Natl. Sci. Nat. Math. Cherbourg, 30:293–304.

1915. Sur la sexualité heterogamique d'une Laminaire (*Saccorhiza bulbosa*). Compt. Rend. Acad. Sci. [Paris], 161:769–799, 3 figs.

1926. Sur un nouveau type d'alternance de générations chez les algues brunes; les Sporochnales. Compt. Rend. Acad. Sci. [Paris], 182:361–364.

1931. Sur quelques algues phéosporées de la rade de Villefranche (Alpes-Maritimes). Bull. Stat. Biol. Arcachon, 28:7-168, 32 figs.

SCHECHNER-FRIES, MARGARETE

1934. Der Phasenwechsel von *Valonia utricularis* (Roth) Ag. österr. Bot. Zeitschr., 83:241–254, 3 figs.

SCHERFFEL, A.

1901. Kleiner Beitrag zur Phylogenie einiger Gruppen niederer Organismen. Bot. Zeit., 59:143–158, pl. 6.

1911. Beitrag zur Kenntnis der Chrysomonadineen. Archiv Protistenk., 22:229–344, pl. 16.

1924. Über die Cyste von *Monas*. Archiv Protistenk., 48:187–195, 6 figs.

1927. Beitrag zur Kenntnis der Chrysomonadineen. II. Archiv Protistenk., 57:331–361, 3 figs., pl. 15.

SCHIFFNER, V.

1926. Die Existenzgründe der Zellbildung und Zellteilung, der Vererbung und Sexaulität . . . iv + [1] + 160 pp. Jena: G. Fischer.

SCHILLER, J.

1925a. Die planktontischen Vegetationen des adriatischen Meeres. A. Die Coccolithophoriden-Vegetation in den Jahren 1911–14. Archiv Protistenk., 51:1–130, 24 figs., 11 tables, pls. 1-9.

1925b. Die planktontischen Vegetationen des adriatischen Meeres. B. Chrysomonadina, Heterokontae, Cryptomonadina, Eugleninae, Volvocales. 1. Systematischer Teil. Archiv Protistenk., 53:59–123, 30 figs., pls. 3–6.

1926. Über Fortpflanzung, geissellose Gattungen und die Nomenklatur der Coccolithophoraceen nebst Mitteilung über Copulation bei *Dinobryon*. Archiv Protistenk., 53:326–342, 8 figs.

1930. Coccolithineae. *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, österreich und der Schweiz. 2nd ed. Bd. 10, Abt. 2 (issued by R. Kolkwitz). Pp. 89–273, figs. 1–139, A–F. Leipzig: Akad. Verlagsges.

1931–1933. Dinoflagellatae (Peridineae). *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, österreich und der Schweiz. 2nd ed. Bd. 10, Abt. 3, Teil 1 (issued by R. Kolkwitz). vi + 617 pp., 631 figs. Leipzig: Akad. Verlagsges.

1935–1937. Dinoflagellatae (Peridineae). *In* L. Rabenhorst's Kryptogamen-Flora von Deutschland, österreich und der Schweiz. 2nd ed. Bd. 10, Abt. 3, Teil 2 (issued by R. Kolkwitz). vii + 589 + [1] pp., 612 figs. Leipzig: Akad. Verlagsges.

SCHILLING, A. J.

1913. Dinoflagellatae (Peridineae). *In* A. Pascher, Die Süsswasserflora Deutschlands, österreichs und der Schweiz. Heft 3. iv + 66 pp., 69 figs. Jena: G. Fischer.

SCHMIDLE, W.

1903. Bemerkungen zu einigen Süsswasseralgen. Ber. Deutsch. Bot. Ges., 21:346–355, pl. 18.

SCHMIDT, O. C.

1937a. Choristocarpaceen und Discosporangiaceen. Hedwigia, 77(1):1–4.

1937b. Die Masonophyceen, eine neue Familie der Braunalgen. Hedwigia, 77(1):5–6.

1938. Beiträge zur Systematik der Phaeophyten I. Hedwigia, 77(5, 6):213–230.

SCHMITZ, C. J. F.

1879a. Ueber grüne Algen im Golf von Athen. Sitzungsber. Naturf. Ges. Halle (Sitzung am. 30. Nov. 1878), pp. 17–23. (Reprinted under the title "Ueber grüne Algen aus dem Golf von Athen" in Bot. Zeit., 37:167–175, 1879.)

1879b. Untersuchungen über die Fruchtbildung der Squamarieen. Sitzungsber. Niederrhein. Ges. Natur- u. Heilkunde Bonn (in Verh. Naturhist. Ver. Preuss. Rheinlande u. Westfalens), 36:376–377.

1879c. Untersuchungen über die Zellkerne der Thallophyten. Sitzungsber. Niederrhein. Ges. Natur- u. Heilkunde Bonn, 1878:345–376.

1882. Die Chromatophoren der Algen. Vergleichende Untersuchungen über Bau und Entwicklung der Chlorophyllkörper und analogen Farbstoffkörper der Algen. iv + 180 pp., 2 pls. Bonn: Max Cohen and Sohn. (Also in Verh. Naturhist. Ver. Preuss. Rheinl. Westfal., 40(1883):1–180, pls. 1, 2.)

1883. Untersuchungen über die Befruchtung der Florideen. Sitzungsber. K. Preuss. Akad. Wiss. Berlin, 1883(1):215–258, pl. 5.

1889. Systematische Übersicht der bisher bekannten Gattungen der Florideen. Flora, 72:435–456, pl. 21.

SCHMITZ, C. J. F., and P. HAUPTFLEISCH

1896–1897. Rhodophyceae. *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . Teil 1, Abt. 2. Pp. 298–544, figs. 192–288. Leipzig: W. Engelmann.

SCHULZ, P.

1928. Beiträge zur Kenntnis fossiler und rezenter Silicoflagellaten. Bot. Archiv, 21:225–292, 83 figs.

SCHULZE, K. L.
1939. Cytologische Untersuchungen an *Acetabularia mediterranea* und *Acetabularia wettsteinii*. Archiv Protistenk., 92:179–225, 20 figs., pls. 11, 12.

SCHUSSNIG, B.
1925. Betrachtungen über das System der niederen Pflanzen. Verh. Zool.-Bot. Ges. Wien, 74–75; 196–272.
1930. Der Generations- und Phasenwechsel bei den Chlorophyceen. (Ein historicher Rückblick.) österr. Bot. Zeitschr., 79:58–77.
1932. Der Generations- und Phasenwechsel bei den Chlorophyceen III. österr. Bot. Zeitschr., 81:296–298.
1938. Der Kernphasenwechsel von *Valonia utricularis* (Roth) Ag. Planta., 28:43–59, 3 figs.
1939. Ein Beitrag zur Entwiklungsgeschichte von *Caulerpa prolifera*. Bot. Not. 1939: 75–96, 6 figs.
1950. Die Gametogenese von *Codium decorticatum* (Woodw.) Howe. Svensk Bot. Tidskr., 44:55–71, 2 figs., pls. 1, 2.

SCHÜTT, F.
1888. Ueber die Diatomeengattung *Chaetoceros*. Bot. Zeit., 46:161–170, 177–184, pl. 3.
1895. Die Peridineen der Plankton-Expedition. I. Theil. Studien über die Zellen der Peridineen. Ergebnisse der Plankton-Expedition der Humboldt-Stiftung. Bd. iv. M. a. A. 170 pp., 27 pls. Kiel and Leipzig: Lipsius and Tischer.
1896. Gymnodiniaceae, Prorocentraceae, Peridiniaceae, Bacillariaceae. *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . (continued by A. Engler). Teil 1, Abt. 1b. 153 pp., 282 figs. Leipzig: W. Engelmann.

SCHWARZ, ELISABETH
1932. Beiträge zur Entwicklungsgeschichte der Protophyten. IX. Der Formwechsel von *Ochrosphaera neapolitana*. Archiv Protistenk., 77:434–462, 7 figs., pl. 13.

SENN, G.
1900. Flagellata. *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . Teil I, Abt 1a. Pp. 93–188, figs. 63–140. Leipzig: W. Engelmann.

SETCHELL, W. A.
1929. The genus *Microdictyon*. Univ. Calif. Publ. Bot., 14(20):453–588, 105 figs.

SETCHELL, W. A., and N. L. GARDNER
1919. The marine algae of the Pacific coast of North America. Pt. 1, Myxophyceae. Univ. Calif. Publ. Bot., 8(1):1–138, incl. pls. 1–8.
1920. The marine algae of the Pacific coast of North America. Pt. 2. Chlorophyceae. Univ. Calif. Publ. Bot., 8(2):139–375, incl. pls. 9–33.
1922. Phycological contributions. VI. New species of *Ectocarpus*. Univ. Calif. Publ. Bot., 7(11):403–427, incl. pls. 45–49.
1925. The marine algae of the Pacific coast of North America. Pt. 3. Melanophyceae. Univ. Calif. Publ. Bot., 8(3):383–898, incl. pls. 34–107.

SEYBOLD, A., K. EGLE, and W. HÜLSBRUCH
1941. Chlorophyll- und Carotinoidbestimmungen von Süsswasseralgen. Bot. Archiv, 42:239–253, 6 tables.

SIEBOLD, C. T. VON
1848. Wirbellose Thiere. *In* C. T. Siebold and H. Stannius, Lehrbuch der vergleichenden Anatomie. Vol. 1. xiv + 679 + [1] pp. Berlin: Veit and Co.
1849. Ueber einzellige Pflanzen und Thiere. Zeitschr. Wiss. Zool., 1:270–294.

SILVA, P. C.

1952. A review of nomenclatural conservation in the algae from the point of view of the type method. Univ. Calif. Publ. Bot., 25(4):241–323.

SILVA, P. C., and R. C. STARR

1953. Difficulties in applying the international code of botanical nomenclature to certain unicellular algae, with special reference to *Chlorococcum*. Svensk Bot. Tidskr., 47:235–247.

SINGH, R. N.

1945. Nuclear phases and alternation of generations in *Draparnaldiopsis indica* Bharadwaja. New Phytol., 44:118–129, 49 figs.

1947. *Fritschiella tuberosa* Iyeng. Ann. Bot., n. s., 11:159–164, 11 figs.

SJÖSTEDT, L. G.

1926. Floridean studies. Lunds Univ. Årsskr., N. F., Avd. 2, 22(4). 95 pp., 41 figs.

SKOTTSBERG, C.

1907. Zur Kenntnis der subantarktischen und antarktischen Meeresalgen. I. Phaeophyceen. Wiss. Ergebn. Schwed. Südpolar-Exped. 1901–1903. Bd. 4(6). 172 pp., 187 figs., 10 pls., 1 map. Stockholm: Norstedt and Söner.

SKUJA, H.

1938. Die phylogenetischen Entwicklungsrichtungen bei den Protisten. Acta Biol. Latvica, 8:1–26.

1939a. Versuch einer systematischen Einteilung der Bangioideen oder Protoflorideen. Acta Hort. Bot. Univ. Latviensis, 11–12:23–40.

1939b. Beitrag zur Algenflora Lettlands II. Acta Hort. Bot. Univ. Latviensis, 11–12: 41–169, pls. 1–11.

1948. Taxonomie des Phytoplanktons einiger Seen in Uppland, Schweden. Symb. Bot. Upsal., Vol. 9(3). 399 pp., 39 pls.

1950. Körperbau und Reproduktion bei *Dinobryon Borgei* Lemm. Svensk Bot. Tidskr., 44:96–107, 1 fig.

SMITH, G. M.

1920. Phytoplankton of the Inland Lakes of Wisconsin. Pt. I, Myxophyceae, Phaeophyceae, Heterokonteae, and Chlorophyceae exclusive of the Desmidiaceae. Wis. Geol. Nat. Hist. Surv., Sci. Ser. No. 12. 243 pp., 2 tables, 51 pls. Madison, Wis.: Publ. by the State.

1930. Observations on some siphonaceous green algae of the Monterey Peninsula. *In* Contributions to Marine Biology. Pp. 222–233, 3 figs. Stanford Univ. Press.

1933. The Fresh-water Algae of the United States. xi + 716 pp., 449 figs., 2 tables. New York and London: McGraw-Hill.

1938. Cryptogamic Botany. Vol. I. viii + 545 pp., 299 figs. New York and London: McGraw-Hill.

1944. Marine Algae of the Monterey Peninsula California. vii + [1] + 622 pp., incl. 98 pls. Stanford Univ. Press.

1950. The Fresh-water Algae of the United States. 2nd ed. vii + 719 pp., 559 figs., 3 tables. New York, Toronto, London: McGraw-Hill.

SOLMS-LAUBACH, H.

1867. Ueber die Fruchtentwickelung von *Batrachospermum*. Bot. Zeit., 25:161–167, 169–171, pl. 4.

STACKHOUSE, J.

1795–1801. Nereis britannica . . . xi + 112 + [7] pp., 17 +A–G pls. Bath: Hazard.

1809. Tentamen marino-cryptogamicum . . . Mém. Soc. Imp. Nat. Moscou, 2:50–97.

1816. Nereis britannica . . . 2nd ed. xii + 68 pp., 20 pls. Oxford: Collingwood.

Stanier, R. Y., and C. B. van Niel

1941. The main outlines of bacterial classification. Journ. Bact., 42:437–466, 2 figs.

Stein, F. von

1878. Der Organismus der Infusionsthiere . . . Abt. 3. Die Naturgeschichte der Flagellaten oder Geisselinfusorien. I. Hälfte. Den noch nicht abgeschlossenen allgemeinen Theil nebst Erklärung der sämmtlichen Abbildungen enthaltend. x + 154 pp., 24 pls. Leipzig: W. Engelmann.

1883. Der Organismus der Infusionstheire . . . Abt. 3. Die Naturgeschichte der Flagellaten oder Geisselinfusorien. II. Hälfte. Die Naturgeschichte der arthrodelen Flagellaten. 30 pp., 25 pls. Leipzig: W. Engelmann.

Steinecke, F.

1932. Algologische Notizen II. *Heterodendron Pascheri, Euglenocapsa ochracea, Stylodinium cerasiforme.* Archiv Protistenk, 76:589–594, 3 figs.

Stizenberger, E.

1860. Dr. Ludwig Rabenhorst's Algen Sachsens resp. Mitteleuropa's Decade I–C. Systematisch geordnet (mit Zugrundelegung eines neuen Systems). 41 pp. Dresden: Heinrich.

Stosch, H. A.

1951a. Entwicklungsgeschlichtliche Untersuchungen an zentrischen Diatomeen I. Die Auxosporenbildung von *Melosira varians.* Archiv. Mikrobiol., 16:101–135, inc. 2 pls. and 22 figs.

1951b. Zur Entwicklungsgeschichte zentrischer Meeresdiatomeen. Naturwiss., 38: 191–192.

Strain, H. H.

1948. Occurrence and properties of chloroplast pigments. Carnegie Inst. Washington Year Book No. 47, pp. 97–100.

1951. The pigments of algae. *In* G. M. Smith, ed., Manual of Phycology . . . Pp. 243–262, 7 tables. Waltham, Mass.: Chronica Botanica Co.

Strasburger, E.

1887. Das botanische Practicum. 2nd ed. xxxvi + 685 pp., 193 figs. Jena: G. Fischer.

1897. Kernteilung und Befruchtung bei *Fucus.* Jahrb. Wiss. Bot., 30:351–374, pls. 17, 18.

Strehlow, K.

1929. Über die Sexualität einiger Volvocales. Zeitschr. Bot., 21:625–692, 17 figs.

Strömfelt, H. F. G.

1886. Om algvegetationen vid Islands kuster. 89 pp., 1 table, 3 pls. Thesis (Upsala). Gothenburg: Publ. by author.

Sturch, H. H.

1926. *Choreocolax Polysiphoniae* Reinsch. Ann. Bot., 40:585–605, 15 figs.

Subrahmanyan, R.

1946. On the occurrence of microspores in some centric diatoms of the Madras coast. Journ. Indian Bot. Soc., 25:61–66, 12 figs., pl. 4.

1947. On somatic division, reduction division, auxospore-formation and sex-differentiation in *Navicula halophila* (Grun.) Cl. M. O. P. Iyengar Comm. Vol., Journ. Indian Bot. Soc., pp. 239–266, 81 figs., pls. 1, 2.

Suneson, S.

1947. Notes on the life-history of *Monostroma.* Svensk Bot. Tidskr., 41:235–246, 2 figs., 1 table.

SVEDELIUS, N.

1915. Zytologisch-entwicklungsgeschichtliche Studien über *Scinaia furcellata* ein Beitrag zur Frage der Reduktionsteilung der nicht tetrasporenbildenden Florideen. Nova Act Reg. Soc. Sci. Upsal., ser. 4, 4(4). 55 pp., 32 figs.

1916. Das Problem des Generationswechsels bei den Florideen. Naturwiss. Wochenschr., N. F., 15:353–359, 372–379, 14 figs.

1942. Zytologisch-entwicklungsgeschichtliche Studien über *Galaxaura* eine diplobiontische Nemalionales-Gattung. Nova Acta Reg. Soc. Sci. Upsal., ser. 4, 13(4). 154 pp., 80 figs.

1953. Critical studies on some species of *Galaxaura* from Hawaii. Nova Acta Reg. Soc. Sci. Upsal., ser. 4, 15(9). 92 pp., 70 figs.

TANAKA, T.

1952. The systematic study of the Japanese Protoflorideae. Mem. Fac. Fisheries Kagoshima Univ., vol. 2(2). 92 pp., 41 figs., pls. 1–23.

THURET, G.

1840. Note sur l'anthère du *Chara* et les animalcules qu'elle renferme. Ann. Sci. Nat. Bot., sér. 2, 14:65–72, pls. 5–8.

1850. Recherches sur les zoospores des algues et les anthéridies des cryptogames. Première partie.—Zoospores des algues. Ann. Sci. Nat. Bot., sér. 3, 14:214–260, pls. 16–31.

1851. Recherches sur les zoospores des algues et les anthéridies des cryptogames. Seconde partie.—Authéridies des cryptogames. Ann. Sci. Nat. Bot., sér. 3, 16:5–39, pls. 1–15.

1853a. Sur la fécondation des Fucacées. Compt. Rend. Acad. Sci. [Paris], 36:745–748.

1853b. Note sur la fécondation des Fucacées. Mém. Soc. Sci. Nat. Cherbourg, 1:161–167.

1854. Recherches sur la fécondation des Fucacées, suivies d'observations sur les anthéridies des algues. Ann. Sci. Nat. Bot., sér. 4, 2:197–214, pls. 12–15.

1855. Recherches sur la fécondation des Fucacées et les anthéridies des algues. II. Ann. Sci. Nat. Bot., sér. 4, 3:5–28, pls. 2–4.

1875. Essai de classification des Nostochinées. Ann. Sci. Nat. Bot., sér. 6, 1:372–382.

THURET, G., and É. BORNET

1878. Etudes phycologiques. iii + 105 pp., 51 pls. Paris: Masson.

THWAITES, G. H. K.

1847. On conjugation in the Diatomaceae. Ann. Mag. Nat. Hist., 20:9–11, 343–344, pls. 4, 22.

1848. Further observations on the Diatomaceae; with descriptions of new genera and species. Ann. Mag. Nat. Hist., ser. 2, 1:161–172, pls. 11, 12.

TIFFANY, L. H.

1930. The Oedogoniaceae, . . . 253 pp., incl. 64 pls. Publ. by author.

TILDEN, JOSEPHINE E.

1933. A classification of the algae based on evolutionary development, with special reference to pigmentation. Bot. Gaz., 95:59–77, pl. 1.

1935. The Algae and their Life Relations. xii + 550 pp., 257 figs., frontis. Minneapolis: Univ. Minnesota Press.

TONI, J. B. DE

1888. Conspectus generum chlorophycearum hucusque cognitorum. Notarisia, 3:447–453.

1889. Sylloge algarum . . . Vol. 1. Chlorophyceae. 12 + cxxxix + 1315 pp. Padua: Publ. by author.

TONI, J. B. DE (Cont.)

1890. Osservazioni sulla tassonomia delle Bacillariee (Diatomee) seguite da un prospette dei generi delle medesime. Notarisia, 5:885–922.

1891a. Sylloge algarum . . . Vol. 2, Bacillarieae, Sec. I, Raphideae. cxxxii + 490 pp. Padua: Publ. by author.

1891b. Systematische Uebersicht der bisher bekannten Gattungen der echten Fucoideen. Flora, 74:171–182.

1892. Sylloge algarum . . . Vol. 2, Bacillarieae, Sec. II, Pseudoraphideae. Pp. 491–817. Padua: Publ. by author.

1894. Sylloge algarum . . . Vol. 2, Bacillarieae, Sec. III, Cryptorhaphideae. Pp. 819–1556. Padua: Publ. by author.

1895. Sylloge algarum . . . Vol. 3, Fucoideae. xvi + 638 pp. Padua: Publ. by author.

1897. Sylloge algarum . . . Vol. 4. Florideae, Sec. 1. xx + lxi +386 + [2] pp. Padua: Publ. by author.

TRANSEAU, E. N.

1951. The Zygnemataceae. xiv + 327 pp., incl. 41 pls. Columbus: Ohio State Univ. Press.

TURNER, D.

1802. A Synopsis of the British Fuci. Vols. 1 and 2. xlvi + 400 pp. London: White.

1808. Fuci . . . Vol. 1. 164 + [2] pp., pls. 1–71. London: Arch.

1809. Fuci . . . Vol. 2. 162 + [2] pp., pls. 72–134. London: Arch.

1811. Fuci . . . Vol. 3. 148 + [2] pp., pls. 135–196. London: Arch.

1819. Fuci . . . Vol. 4. [1] + 153 + [2] + 7 pp., pls. 197–258. London: Arch.

TURPIN, P. J. F.

1828a. Aperçu organographique sur le nombre deux. Mém. Mus. Hist. Nat. [Paris], 16:295–344, pl. 13.

1828b. Observations sur le nouveau genre *Surirella*. Mém. Mus. Hist. Nat. [Paris], 16:361–368, pl. 15.

TUTTLE, A. H.

1926. The location of the reduction divisions in a charophyte. Univ. Calif. Publ. Bot., 13(12):227–235, incl. pls. 22, 23.

VAILLANT, S.

1721. Caractères de quatorze genres de plantes; le dénombrement de leurs espèces; les descriptions de quelques-unes, & les figures de plusieurs. Hist. Acad. R. Sci. [Paris], Mém. Math.-Phys., 1719:9–47, 4 pls.

VAUCHER, J. P. É.

1803. Histoire des conferves d'eau douce . . . xv + 285 + [2] pp., 17 pls. Geneva: Paschoud.

1821. Mémoire sur les charagnes. Mém. Soc. Phys. Hist. Nat. Genève, 1:168–179, 1 pl.

VILLARS, D.

1789. Histoire des plantes de Dauphiné. Vol. 3. xxxii + 1091 pp. Grenoble: Publ. by author.

VLK, W.

1931. Über die Struktur der Heterokontengeisseln. Beih. Bot. Centr., 48:214–220, 15 figs.

1938. Über den Bau der Geissel. Archiv Protistenk., 90:448–488, 12 figs., pl 23.

WALLICH, G. C.

1858. On *Triceratium* and some new allied forms, with figures of the same. Quart. Journ. Micr. Sci., 6:242–253, pls. 12, 13.

WALLICH, G. C. (Cont.)

1860a. Results of soundings in the north Atlantic. Ann. Mag. Nat. Hist., ser. 3, 6:457–458.

1860b. On the development and structure of the diatom-valve. Trans. Micro. Soc., n. s., 8:129–145.

1861. Remarks on some novel phases of organic life, and on the boring powers of minute annelids, at great depths in the sea. Ann. Mag. Nat. Hist., ser. 3, 8:52–58, 7 figs.

1865. On the structure and affinities of the Polycystina. Trans. Micro. Soc. London, 13:57–84.

1869. Coccoliths and coccospheres. Quart. Journ. Micr. Sci., 17:77–78.

1877. Observations on the coccosphere. Ann. Mag. Nat. Hist., ser. 4, 19:342–350, pl. 17.

WALLROTH, F. W.

1815. Annus botanicus, sive supplementum tertium ad C. Sprengelii floram halensem. Cum tractatu et iconibus VI Charam genus illustrantibus. xxx + 200 pp., 6 pls. Halle: Kümmel. (Not seen.)

1833. Flora cryptogamica germaniae. Pars posterior [= Vol. 2], continens algas et fungos. lvi + 923 pp. Nürnberg: Schrag.

WALZ, J.

1866–1867. Beitrag zur Morphologie und Systematik der Gattung *Vaucheria* DC. Jahrb. Wiss. Bot., 5:127–160, pls. 12–14.

WARMING, E.

1876. Om nogle ved Danmarks kyster levende Bakterier. Videnskab. Medd. Dansk Naturhist. Foren. Kjøbenhavn, 1875:307–420, pls. 7–10.

1890. Handbuch der systematischen Botanik. (Translated from the 2nd Danish ed., 1884, by E. Knoblauch.) xii + 468 pp., 573 figs. Berlin: Gebr. Borntraeger.

WEISMANN, A.

1887. Ueber die Zahl der Richtungskörper und über ihre Bedeutung für die Vererbung. viii + 75 pp. Jena: G. Fischer.

WEST, G. S.

1904. A Treatise on the British Fresh-water Algae. xv + 372 pp., 166 figs., frontis. Cambridge Univ. Press.

1916. Algae. Vol. 1 [only vol. published]. viii + [2] + 475 pp., 271 figs. Cambridge Univ. Press.

1927. A Treatise on the British Fresh-water Algae . . . Rev. ed. by F. E. Fritsch. xvii + [1] + 534 pp., 207 figs., frontis. Cambridge Univ. Press.

WEST, W., and G. S. WEST

1897. Welwitsch's African fresh-water algae. Journ. Bot., 35:1–7, 33–42, 77–89, 113–122, 172–183, 235–243, 264–272, 297–304, pls. 365–370.

WETTSTEIN, R. R.

1901. Handbuch der systematischen Botanik. Bd. 1. ix + [1] + 201 pp., 126 figs. Leipzig and Vienna: Deuticke.

1924. Handbuch der systematischen Botanik. 3rd ed. viii + 1017 + [1] pp., 653 figs. Leipzig and Vienna: Deuticke.

WILLE, N.

1890–1891. Conjugatae [und] Chlorophyceae. *In* A. Engler, Die natürlichen Pflanzenfamilien . . . Teil I, Abt. 2. Pp. 1–175, 128 figs. Leipzig: W. Engelmann.

1894. Ueber die Befruchtung bei *Nemalion multifidum* (Web. et Mohr) J. Ag. Ber. Deutsch. Bot. Ges., 12 [Suppl.] : (57)–(60), 6 figs.

WILLE, N. (Cont.)

1900. Algen aus dem nördlichen Tibet, von Dr. S. Hedin im Jahre 1896 gesammelt. Petermanns Mitt. Justus Perthes Geogr. Anstalt, Ergänzungsband 28 (Heft 131), pp. 370–371.

1901. Algologische Notizen VII. Zur Verbreitung der Süsswasseralgen im südlichen Norwegen. Nyt. Mag. Naturvidenskab., 39:1–22.

1909a. Algologische Notizen XV. Über *Wittrockiella* Nov. Gen. Nyt. Mag. Naturvidenskab., 47:209–225, pls. 11–14.

1909b. Conjugatae und Chlorophyceae. *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien . . . Nachträge zum I. Teil, Abt. 2. Pp. 1–136, figs. 1–70. Leipzig: W. Engelmann.

WILLIAMS, J. L.

1904a. Studies in the Dictyotaceae. I. The cytology of the tetrasporangium and the germinating tetraspore. Ann. Bot., 18:141–160, pls. 9, 10.

1904b. Studies in the Dictyotaceae. II. The cytology of the gametophyte generation. Ann. Bot., 18:183–204, pls. 12–14.

WILLIAMS, MAY M.

1925. Contributions to the cytology and phylogeny of the siphonaceous algae. I. The cytology of the gametangia of *Codium tomentosum* (Stack.). Proc. Linn. Soc. New South Wales, 50(2):98–111, 42 figs.

WITTROCK, V. B.

1877. On the development and systematic arrangement of the Pithophoraceae, a new order of algae. Nova Acta Reg. Soc. Sci. Upsal., extra ord. vol. (Art. 19). 80 pp., 6 pls.

WOOD, R. D.

1952. The Characeae, 1951. Bot. Rev., 18:317–353.

WORONIN, M.

1869. Beitrag zur Kenntniss der Vaucherien. Bot. Zeit., 27:137–144, 153–162, pls. 1, 2.

YAMANOUCHI, S.

1906a. The life history of *Polysiphonia violacea*. Bot. Gaz., 41:425–433.

1906b. The life history of *Polysiphonia violacea*. Bot. Gaz., 42:401–449, 3 diagrams, pls. 19–28.

1909a. Mitosis in *Fucus*. Bot. Gaz., 47:173–197, pls. 8–11.

1909b. Cytology of *Cutleria* and *Aglaozonia* (a preliminary paper). Bot. Gaz., 48: 380–386.

1911. On the life history of *Zanardinia collaris* Crouan. (A preliminary note.) Bot. Mag. Tokyo, 25:9–11. (In Japanese.)

1912. The life history of *Cutleria*. Bot. Gaz., 54:441–502, 15 figs., pls. 26–35.

1913. The life history of *Zanardinia*. Bot. Gaz., 56:1–35, 24 figs., pls. 1–4.

ZANARDINI, J.

1843. Saggio di classificazione naturale delle ficee. 65 + [1] pp., 3 charts, 1 pl. Venice: Publ. by author.

ZANEVELD, J. S.

1940. The Charophyta of Malaysia and adjacent countries. Blumea, 4(1):1–223, 21 figs., 16 tables.

ZIMMERMANN, W.

1930. Neue und wenig bekannte Kleinalgen von Neapel I–V. Zeitschr. Bot., 23:419–442, 11 figs., pl. 1.

ZINNECKER, EMMI

1935. Reduktionsteilung, Kernphasenwechsel und Geschlechtsbestimmung bei *Bryopsis plumosa* (Huds.) Ag. österr. Bot. Zeitschr., 84:53–72, 6 figs.

MYCOLOGY

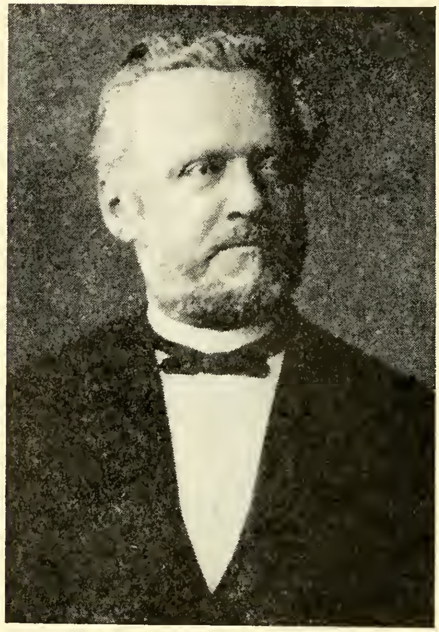
By ERNST ATHEARN BESSEY
Michigan State College, East Lansing

THE WORD "MYCOLOGY," applied to the study of fungi, is not very many years older than the beginning of the hundred-year period covered by this series of papers. In the Latin form, *mycologia,* it was used by Persoon (1801). As an English word, according to Murray (1908), it was first used by the Reverend Miles Joseph Berkeley in 1846 in *British Flora, Fungi,* in which, also, he applied the term "mycologist" to the students of fungi. In 1850 Fresenius used the word in the German form. After that it came into general usage in European publications in France and Italy, as well as in England and Germany, though in England the word "fungology" was frequently used, a term introduced by Berkeley in 1860.

Fungi were known to the ancients. Indeed the Emperor Nero was very fond of eating the mushroom *Amanita caesarea* Schaff. ex. Fr., the specific epithet being given because of this fact. In the seventeenth and eighteenth centuries the larger fungi attracted the attention of botanists more and more but it was not until the publication of the works of Christiaan Hendrik Persoon (1801, 1822–1828) and Elias Magnus Fries (1821–1832 and many subsequent publications until about the time of his death in 1878) that the larger fungi were studied extensively as well as intensively. The microscopic fungi were mostly given scant attention or entirely passed over until the improvements of the compound microscope made it possible to study their structure and to begin to form systems of classification for them. The path-breaking work of Corda (1837–1854) was scarcely completed by the middle of the last century. By the use of the microscope and the numerous illustrations in his great work, he added thousands of microscopic or semimicroscopic species to our knowledge.

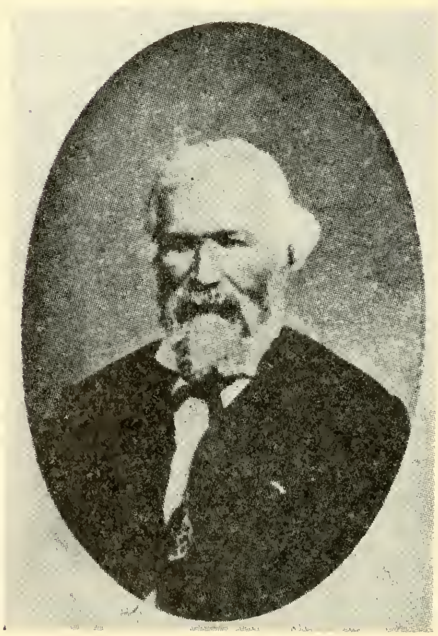
It must be remembered that one hundred years ago many botanists and other students of natural history believed that the small fungi occurring on or within the tissues of plants and animals were not distinct beings but actually modifications of the diseased tissues of the host organisms, or "exanthemata." This was the view held by Elias Magnus Fries (1821–1832, 1836–1838), and Friedrich Wilhelm Wallroth (1833). In this same year Franz Josef Andreas Nicolaus Unger, in one of the earlier books on phytopathology, *Die Exanthème der Pflanzen* (1833), supported these ideas. Twenty years later the English botanist, John Lindley, in his book *The Vegetable Kingdom,* although apparently questioning the development of fungi by other means than from spores, asserts that many botanists still hold to the views of Fries and Unger. Yet he doubts the ability of fungi to cause plant disease, indicating that they enter tissues already diseased from other causes, such as extreme moisture, drought, malnutrition, and so forth. This whole question is very dramatically set forth by Large in his very

PIER ANDREA SACCARDO
1845–1920



SIMON SCHWENDENER
1829–1919

ROLAND THAXTER
1858–1932



LOUIS RENÉ TULASNE
1815–1885

interesting book *Advance of the Fungi* (1940), especially with reference to the great epiphytotic of late blight of the potato. In 1845 when this attacked the crops of Great Britain and Ireland and other parts of Europe there were two opposed groups of scientists. One, headed by Berkeley, insisted that the fungus associated with the disease (later named *Phytophthora infestans* [Mont.] De Bary) was the real cause of the trouble, whereas the other group, led by Lindley, maintained that the disease came first and was due to soil or weather conditions or to the "running out" of the varieties. As for the ever-present fungus, some held with Lindley that it was simply growing upon the already diseased tissue, but was not the cause of the disease. Others agreed with Unger and Fries in considering the fungus the product of the diseased tissue.

The Structure and Life History of Fungi

In Great Britain Berkeley was for many years the leading student of fungi, including those whose study required the use of the compound microscope. He described many hundreds of species of hitherto unrecognized fungi and was the backbone of the group which maintained that many of the smaller fungi were actual parasites (in the present sense of the word) upon the hosts. On the Continent, after Corda's death in 1849, the study of the smaller fungi as well as of the structure of the larger fungi was carried on by Joseph Henri Léveillé (who lived from 1796 to 1870), and very many were carefully described and illustrated by him, even though he still maintained that they originated as exanthemata upon the host plants and were not really parasites. But the researches of Berkeley, Fresenius, and especially Montagne (b. 1784, d. 1866) and Tulasne, rapidly brought the scientific world to abandon this idea. Persoon (1801) said, it is true, of some fungi, "*Locus natalis . . . in plerisque parasiticus est ut pleraeque plantae aphyllae parasiticae sunt,*" but it is not certain whether he regarded a parasite as we do as obtaining its nourishment at the expense of, and causing injury to, its host, or whether he used the term in the old classical sense of a person obtaining his meals at the table of another. Schleiden in the third edition of his *Grundzüge der Wissenschaftlichen Botanik* (1850) took a midway position on the question. He did not regard the rusts and smuts as independent organisms but only as diseases of plants. On the contrary, the fungi which grew in the intercellular passages of their hosts and emerged through the stomata he considered true parasitic plants. His work was the leading botanical textbook in Germany and had great influence upon the ideas of students of mycology. However, since he did not publish descriptions of new species of fungi, it remained, apparently, without much influence upon mycological systematists, who did little in the way of careful intensive study of the structure and life histories of the individual fungi.

This newer method of the study of fungi was undertaken in France by Louis René Tulasne (b. 1815, d. 1885) and his brother Charles (b. 1816, d. 1884). The former did the more intensive mycological study, the latter made the marvelously beautiful illustrations for their publications. It soon became apparent to them that some fungi had more than one type of spores and that these did not always germinate in a similar manner. In 1853 they demonstrated that spores of some rusts germinated by the formation of long hyphae or germ tubes and that others produced upon germination hyphae of limited growth (which they called "promycelia"), which bore usually four "sporidia." In 1854 came the discovery that the spores of the genus *Uredo* were only one stage of the development of a rust, the teleutospores (*Puccinia, Uromyces, Coleosporium, Melampsora,* etc.) being produced later by the same mycelium that had given rise to the uredospores. These rusts, therefore, had three spore forms, which we now call urediospores, teliospores, and sporidia (or basidiospores). The Tulasne brothers suggested that the absolute proof of this could only be obtained by controlled inoculation experiments which they had not made and which they believed would be very difficult to carry out successfully. In their *Selecta Fungorum Carpologia* (1861–1865)—perhaps the most sumptuous work of the period, with illustrations whose artistic excellence has never been equaled—were demonstrated the various forms of reproduction of different fungi. It must be admitted that some of the various spore forms which the authors attributed to the fungi so beautifully and accurately illustrated were due to contamination by saprophytes or even parasites, which had nothing to do with the life histories of the fungi under study. Thus a pycnidial stage was described and illustrated for the Erysiphaceae, but later this was demonstrated by De Bary and Woronin (1870) to be a parasitic imperfect fungus, *Cicinnobolus,* growing and producing its own pycnidia within the hyphae of the Erysiphaceae.

Hence it became more and more evident that it was necessary to grow the fungi whose life history was under study from spore to maturity in pure cultures, free from the opportunity of access by other organisms. Due credit for the early making of cultures of fungi should be given to the Italian Pier' Antonio Micheli, who lived from 1679 to 1737. In his great work (1729) he described cultures on suitable vegetable media, using the spores of fungi that he called *Mucor, Aspergillus,* and *Botrytis.* The media were kept covered by bell-jars and developed only the fungus whose spores were sown upon them whereas similar pieces, not thus covered, developed *"Mucor."* Micheli's conclusion was that the spores of these various molds were normally distributed through the air.

The pure-culture study method was in modern times first carried out successfully by Anton De Bary. He was born in 1831, the son of a busy physician in Frankfurt a. M., Germany. He obtained his M.D. degree at the University of Berlin at the age of twenty-two and immediately entered upon the practice of medicine in his home city. He admitted later that the diseases of his patients interested him only until he was sure of the correctness of his diagnosis, and so he soon gave up his practice, as he jokingly remarked *"im Interesse der Kranken."* In December, 1853, he became Privatdozent for botany in the medical faculty of the University of Tübingen. His biographer, Ludwig Jost (1930), states that he remained there only two years, *"zweifellos weniger Kolleg lesend als forschend tätig."* He then accepted a call as Professor at the University of Freiburg, remaining there twelve years and gathering around him a coterie of eager students. In 1867 he was called to the University of Halle a. S. where he remained until his appointment in 1872 to the chair of botany at the newly founded University of Strasburg, a position that he held until his death in 1888.

The botanical laboratory that he established at Freiburg in 1855 was one of the first half-dozen botanical laboratories in the world. He attracted students from many countries by his own boundless energy and by the inspiration which impelled them to tireless research. By his scrupulous exactness of observation and teaching he gave to his students and to the readers of his published works a new appreciation of what fungi were and of their relationships. His first publication, in 1852 on *Achlya prolifera,* was a result of research carried on during the last months before he took his final medical examinations and received his degree. This paper was followed in 1853 by a 144-page booklet entitled *Untersuchungen über die Brandpilze* (including at that time the fungi now placed in the orders Ustilaginales, Uredinales, Protomycetales, and Peronosporales). According to Jost, the chief points demonstrated in this second paper were the presence of a mycelium in all these groups from which, in definite ways, arose the characteristic spores. They were not the products of metamorphosed diseased host tissues. This was at a time when many botanists still had the idea that these fungi were the products of the transformation of the diseased tissues of the hosts. It was not until 1863 that De Bary wrote a paper in which he described the course of development of some Peronosporaceae from the formation of the conidia, their germination upon and infection of the host plants, the progress of the fungus in the host, and the formation of the asexual conidia and of the sexual organs, the oögones and antherids. He found the latter organs also in *Eurotium* and followed the development of the perithecium and asci and ascospores. He also demonstrated that the mold known as "*Aspergillus glaucus*" was the asexual phase of *Eurotium.*

The slime molds early attracted his attention (1858, 1859, 1862). He studied the growth of the plasmodium, the formation of the sporangia and spores, the germination of the latter, the formation of the flagellate amoebae, and the origin of the plasmodium. Because the life history of the vegetative phases of development was clearly more animal than vegetable, he changed the name of the group from Myxomycetes to Mycetozoa and boldly asserted that they belonged outside the vegetable kingdom and among the Protozoa. They completely lack mycelium and have a long amoeboid (or plasmodial) stage, hence cannot be placed in the fungi. Although later studies have fully confirmed the validity of De Bary's researches on this group, the majority of botanists have obstinately clung to the old idea that the slime molds are plants belonging to the fungi. Probably the zoologists are partly to blame for not welcoming with enthusiasm their transfer from the realm of botany to that of zoology. Most zoologists, it is true, accept them as animals, but all the important books on the slime molds treat them as plants. (Lister, 1925; Hagelstein, 1944; Martin, 1949.)

De Bary now extended his inoculation studies to the rusts (1863, 1865). He inoculated bean plants. (*Phaseolus vulgaris* L.). He placed the teliospores of *Uromyces* in drops of water on their leaves, putting a bell-jar over the plant to prevent accidental contamination and to maintain the humidity of the air. The resulting infection showed first spermogonia and then aecia, but not the uredia or telia. When, however, he sowed the aeciospores in a similar manner on the same species of host, he obtained uredia and telia. Thus he proved, what some mycologists had suspected, that all five sorts of spores—sporidia, spermatia, aeciospores, urediospores and teliospores—were successive spore forms of the same rust. He could get no infection by using spermatia and made the suggestion that they were perhaps the male cells which, although still continuing to be formed, had lost their function. It must be remembered that it was not until more than sixty years later that J. H. Craigie (1927a, 1927b) demonstrated that the spermatia are really functional male cells. When De Bary sowed the teliospores upon the wheat plants, however, he obtained no infection, although urediospores were effective. Remembering the tradition among the peasants that barberry (*Berberis vulgaris* L.) caused the "blasting" of nearby wheat, he placed the teliospores from wheat upon the barberry leaves and obtained spermogonia and aecia. The mystery was solved. He coined the two terms to be applied to rusts: "heteroecious" for those that alternated on two kinds of not closely related hosts and "autoecious" for those that could develop aecia and telia upon the same host. His study of other rusts demonstrated that there were some in which certain stages were lacking (e.g., aeciospores or urediospores or both), so that only spermogonia and telia occurred, whereas in *Endophyllum* the uredia and telia were lacking and the aeciospores took over the function of the teliospores and germinated by means of a promycelium which bore sporidia.

In his later studies De Bary sought for the sexual organs in the Ascomycetes, Mucorales, etc. To accomplish this he developed methods of growing the fungus from a single spore in pure culture on sterilized liquid or solid media. Oscar Brefeld, one of his students, learned these methods from him and improved upon his technique. He published a series of fifteen *Hefte* entitled *Botanische Untersuchungen . . .* (1872–1912) on various fungi, from the Mucorales, yeasts, various other Ascomycetes, smuts, various other Basidiomycetes, etc. These show great mastery of the methods but reveal that he missed the basic underlying principles taught by De Bary, viz., that these techniques were to be used to discover the facts from which the unbiased conclusions could be drawn. Thus De Bary had clearly shown that sexual reproduction did occur in some Ascomycetes, as he had also demonstrated it in various species of Saprolegniales, Peronosporales, and Mucorales, although in many of these fungi he showed that there was a tendency toward the occurrence of apogamy or parthenogenesis, with the partial or complete loss of the sexual organs. He considered this a downward modification. Brefeld, on the contrary, developed the hypothesis that there was no sexuality in the Ascomycetes or Basidiomycetes. With this in mind he made his cultures to prove the correctness of the hypothesis. When Brefeld did observe what De Bary considered to be sexual organs, he claimed that they had no sexual functions. It must be said, in excuse for his error, that he was so successful in growing his fungi from single spores that he missed the demonstration that would have been convincing, had he mated his cultures of opposite sexual phases. He claimed that there were two evolutionary tendencies that had led from the Phycomycetes to the higher fungi. In both of the lines, sexuality was supposed to have disappeared. The asci in the Ascomycetes were, in his opinion, modifications of the sporangia or zoosporangia while the basidia of the Basidiomycetes were modifications of the conidiophores of those Phycomycetes that produced conidia instead of sporangia. In both these lines he postulated a reduction of the number of spores from indefinite to eight or four in the Ascomycetes or from indefinite to four in the Basidiomycetes. The genera of the former class in which the asci produce many spores, e.g., *Ascoidea, Thelebolus,* and *Monascus,* he placed in the intermediary group, Hemiasci. It must be noted that later studies of *Monascus* demonstrated that this actually produces many eight-spored asci, the dissolution of whose ascus walls sets the ascospores free within the perithecium, so that Brefeld erroneously thought that there was only a single ascus with many spores. Similarly, he postulated an intermediate group, Hemibasidii, for the Ustilaginaceae in which the promycelium is several-celled and produces a variable number of sporidia. This was considered to be an early step toward the promycelium of *Tilletia,* in which there is only one cell and a smaller (but rather variable) number of sporidia is borne at its apex. From that to the Eubasidii, with normally four basidiospores at the top of the one-celled basidium, was the next step. When De Bary criticized these ideas of Brefeld, the latter became bitter and finally began to claim for himself the pure-culture method of the study of fungi (although in his first publications he credited his revered teacher with its invention).

It is interesting that, although Brefeld's contention that sexual reproduction was entirely lacking in the higher fungi was long ago disproved for Ascomycetes and Basidiomycetes (Harper, 1896; Dangeard, 1907), his system of classification, modified to be sure, has long held sway in Germany and elsewhere and was retained in the revised edition of Engler and Prantl in 1928.

The lichens were not studied as intensively by De Bary as the other fungi. Yet because of the similarity of their "gonidia" to free-living algae he suggested (1866) two possibilities as to their function in the lichen: either the mature lichens were the completely developed fruiting conditions of organisms ("gonidia") whose incompletely developed forms were placed among the algae as Nostocaceae, etc., or they are typical algae which had become parasitized by certain fungi of the Ascomycetes. The latter suggestion may well have been what led Simon Schwendener to his interpretation of the role of the fungi and algae in the lichens, which he demonstrated in 1867 and 1868.

Friedrich Wilhelm Zopf (b. 1846, d. 1909) was for many years Professor of Botany at the University of Halle a. S. He made extensive studies on the Chytridiales and other small aquatic fungi parasitic in algae and small animals. His textbook on fungi (1890) was, next to that of De Bary, the outstanding work on the subject for many decades.

I must not fail to call attention to the very extensive mycological work done by the Englishman, Dr. A. H. Reginald Buller, who was for the greater part of his mycological career Professor of Botany at the University of Manitoba. His student work was carried on in England, where he received the B.Sc. and D.Sc. degrees, and at Leipzig, where he obtained the Ph.D. degree. Thus he combined in his training the best of the British and German traditions. His major studies were reported in a series of seven volumes entitled *Researches on Fungi* (1909–1950). These contain detailed reports of his very ingenious experiments and careful observations on the activities and structures of fungi, mainly on Uredinales, Polyporales, and Agaricales, but including also *Pilobolus* among the Mucorales, spore dispersal in the Ascomycetes and other fungi, etc. Besides these seven volumes he published numerous shorter notes of great interest, many of them in the British journal, *Nature.* Many of Buller's students have become prominent mycologists in Canada and the United States.

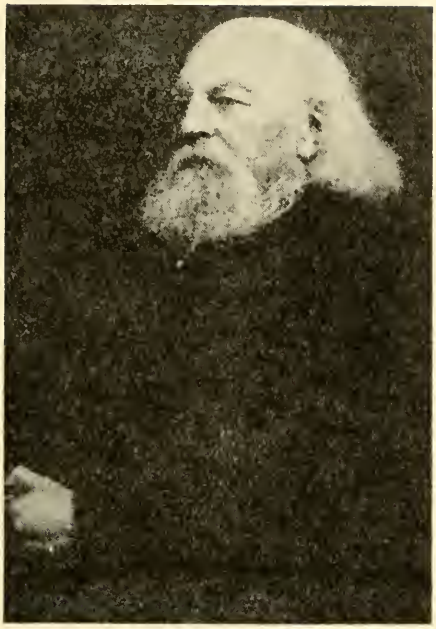
In the foregoing pages I have omitted mention of the studies upon the fungi that attack man and other animals. Some of the forms that attack insects and form external fruiting bodies, e.g., *Cordyceps, Isaria,* etc., were described over two hundred years ago. At first there was a tendency to consider that the appearance above ground of the clavate stroma of *Cordyceps*, emerging from a caterpillar or other buried insect, was but a further development of the insect comparable to the metamorphosis of a pupa to a moth or butterfly. As early as the time of Persoon (1801) and Fries (1821–1832) the clavate stromata were recognized as fungi growing from within the dead insects. Mycotic growths in the air passages of birds were reported between 1815 and 1830. In 1837 Remak (according to Sartory, 1920) reported that in the diseases of man known as thrush and favus the whitish growth was a mass of fungus threads, an observation confirmed two years later by Schoenlein and in 1841 by Gruby (Sartory, 1920). A number of other investigators reported similar discoveries in man and other animals in the next few years. In 1853 appeared the first collective work on these fungi, by Robin. Virchow (1856) described several cases of fungus-infection in the lungs of people and introduced the word mycosis for such infections. From 1860 onward many different mycoses were reported, but mainly this was done by physicians who had little mycological training. It was mainly among the French investigators in the next thirty to forty years that the greatest progress was made in medical mycology.

R. Sabouraud (1894a, 1894b, 1910) made intensive mycological as well as clinical studies of the diseases caused by fungi attacking the hairs in man and other animals—the so-called tineas, ringworms, favus, and so on. E. Bodin (1901), Fernand Guéguen (1909), A Sartory (1920–1923), and Vuillemin (1931) wrote books bringing up to date the accumulated information on these diseases. In Germany, Wilhelm Zopf (1890) devoted a considerable portion of his textbook on fungi to these parasites of man and other animals. In the United States, Dr. Carroll W. Dodge (1935) published a very extensive and detailed work on the subject, probably the most complete up to the date of its publication. Still more recent and clinically more modern is a book by Conant *et al.* (1945). It must be recognized that, except in the last two publications, the mycological nomenclature used is mainly that employed by medical writers, not actually in full accordance with the international rules of botanical nomenclature. Vuillemin admits this in his discussion of the fungi attacking hairs, the "Trichophytes." In recent years the American students of medical mycology have attempted to grow these fungi on standard culture media under, as far as possible, the same conditions of temperature, light, oxygen supply, etc., as are generally used for the culture of plant saprophytes. Thus it has become possible to determine the relationships of a number of these fungi, which, when grown on the special media and at 37° C., produced growths that did not at all reveal their kinship.

It is not only in France and the United States that the study of medical mycology has been progressing. Very much has been accomplished in South America, Italy, Germany, Japan, and in other countries.

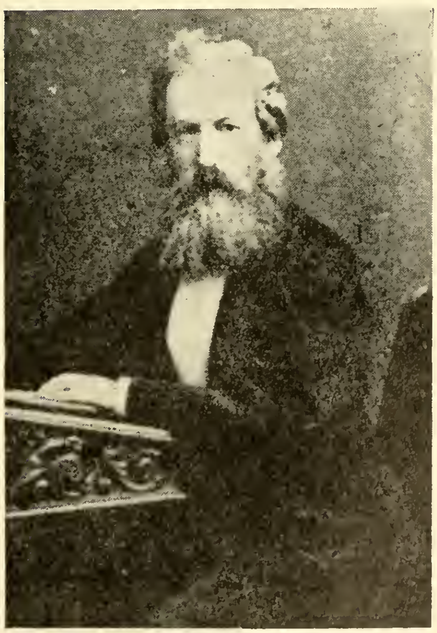
The Taxonomy of Fungi

While all the above-mentioned life-history and anatomical studies, as well as the special studies in medical mycology, were being carried on taxonomy of fungi was not neglected. The earlier European botanical writers included the larger nonmicroscopic fungi in their herbals, but with little idea of their real nature.



MILES JOSEPH BERKELEY
1803–1889

OSCAR BREFELD
1839–1925



MORDECAI CUBITT COOKE
1825–1914

HEINRICH ANTON DE BARY
1831–1888

But with the opening of the eighteenth century there were a few students who gave great care and much time to the study and naming of fungi. Chief among these were Dillenius (1719) and Micheli (1729). These lived respectively from 1687 to 1747 and from 1679 to 1737. Linnaeus (1753) brought together in his twenty-fourth class of plants, Cryptogamia, the fungi whose names and descriptions he had found in the works of his predecessors but, since he knew little about fungi himself, the main value of this portion of his book was the application to these fungi of the binomials instead of the polynomial names of Micheli and Dillenius.

After Linnaeus, the most significant mycological works in the next one hundred years, from the taxonomic viewpoint, were those of Persoon, Fries, and Corda. Christiaan Hendrik Persoon was born in South Africa in 1762. At the age of twelve he was sent by his father to Europe for his education. He never returned to Africa, although he kept in touch with his family and never lost his love for his fatherland. He studied in Holland and Germany and later went to France where he remained until his death. A very interesting account of the ancestry and life of Persoon is given by J. L. M. Franken (1937). The classification of fungi that he used in his *Synopsis Methodica Fungorum* (1801) and his *Mycologia Europaea* (1822–1828) was the foundation upon which the later mycologists based their work. The number of recognized genera and species had been greatly increased. The improvements of the microscope, although it was still a rather crude instrument, made it possible to study the manner in which the spores are borne; thus the fungi could be divided into major groups, many of which are still recognized. It must be remembered that by the International Rules of Botanical Nomenclature the *Synopsis Methodica* is the authoritative work for the names up to 1801 of the Uredinales, Ustilaginales, and Gasteromycetes. Many mycologists believe that it would have been wiser to make that the date of reference for all fungi instead of using Linnaeus (1753), for the Mycetozoa and lichens, and Fries (1821–1832) for the rest of the fungi.

Probably the work of Elias Magnus Fries (b. 1794, d. 1878), especially his *Systema Mycologicum* (1821–1832), along with the above-mentioned publications of Persoon, is what gave the great impetus to the taxonomic study of the larger fungi. For the next one hundred years the classification of the Agaricales and Polyporales especially came to be based upon Fries. One must not forget, however, that he in turn was dependent upon the clarity of vision of his predecessor, Persoon. Fries did not depend greatly upon the microscope so his knowledge of the smaller Ascomycetes and Fungi Imperfecti was not too good.

August Carl Joseph Corda, who lived to be only forty (b. 1809, d. 1849), published a six-volume work, *Icones Fungorum* (1837–1854), in which he described and illustrated hundreds of microscopic fungi, using for that purpose a microscope that we would refuse to consider worth our while but which was good for his time. With the works of Persoon, Fries, and Corda the botanists interested in fungi had at least a fair foundation upon which to build and a beginning of an idea of the structural features basic to taxonomy.

It must be noted that among the foregoing authors there was considerable confusion as to what was meant by the terms "ascus" and "basidium." Apparently Fries did not distinguish between the "ascus" of the genus *Agaricus* and of *Peziza*. He criticized severely the emphasis of differences which could not be distinguished except by the use of a microscope. It was not until about one hundred years ago that the ascus was clearly recognized as the cell *within* which the spores were produced, whereas the basidium had the spores external, or (as Fries considered it) extruded, from the apex of the "ascus." Indeed for many years the word "basidium" was used in a double sense: in the way we now use it as the structure upon which the basidiospores are borne (Berkeley, [1860] used it in this sense); or synonymously for a conidiophore, bearing a cluster of conidia at the apex, which is the usage in the earlier volumes of Saccardo's *Sylloge Fungorum* for the conidiophores or sporophores, as they were called later, of the Sphaeropsidales and Melanconiales. It was not until the publication of Volume XXII of the *Sylloge* in 1913 that the change to these latter terms was made.

A century ago the Reverend Miles Joseph Berkeley (b. 1803, d. 1889) was the leader in taxonomic mycology in England and indeed in almost the whole world. He wrote nearly four hundred papers on mycological topics and gave names to approximately six thousand new species of fungi. As noted previously, at a time when most mycologists considered the microscopic fungi growing upon or within plants to be merely "exanthemata" and not independent entities, he boldly maintained that *Botrytis infestans* Mont. (now known as *Phytophthora infestans*) was the actual cause of the terrible potato disease which caused so much misery and death in Europe, especially in Ireland, in the mideighteenth century. He saw clearly the close connection that ought to exist between "vegetable pathology" and mycology. An account of his life and work, especially in reference to plant diseases is given by Knorr in Phytopathological Classics, No. 8. Among his books may be mentioned *Introduction to Cryptogamic Botany* (1857) and *Outlines of British Fungology* (1860).

Berkeley's successor in the study of fungi in England may be said to have been Mordecai Cubitt Cooke who lived from 1825 to 1914. He wrote the *Handbook of British Fungi* (1871), *Handbook of Australian Fungi* (1892) and numerous contributions to scientific journals. Perhaps his greatest service was the establishment of the periodical *Grevillea*, of which he was the editor and chief contributor for twenty volumes, from 1875 to 1892. Contemporaneous with part of Cooke's life and mycological activity were Worthington G. Smith and George Edward Massee (b. 1850, d. 1917). The latter was the first president of the British Mycological Society, one of the most valuable societies that has been established for the study of fungi. He was the author of *British Fungus-Flora* (1892–1895), *A Textbook of Fungi* (1910), *European Fungus Flora, Agaricaceae* (1902), *Monograph of the Myxogastres* (1892), etc. Since then the number of fungus taxonomists in Great Britain has grown rapidly. It is impossible to mention more than a very few: Elizabeth M. Blackwell, Arthur Disbrowe Cotton, R. W. J. Dennis, Arthur and Gulielma Lister, E. W. Mason, Arthur A. Pearson, Thomas Petch, Carleton Rea, and Ethel M. Wakefield.

The Commonwealth (formerly Imperial) Mycological Institute, in addition to functioning as a center for the plant pathology research of the Commonwealth, numbers among its staff workers who are carrying on a very large amount of taxonomic mycology of the highest excellence.

Joseph Henri Léveillé (b. 1796, d. 1870) was one of the outstanding mycologists in France about one hundred years ago. He studied the nature of the hymenium of the Hymenomycetes and introduced the term "basidium" in its present usage as long ago as 1837. He published in 1851 a report on the taxonomy of the Erysiphaceae. Following his lead and that of the Tulasne brothers there arose in France many systematic mycologists. Space permits the naming of only a few: Philippe van Tieghem, Émile Boudier, Paul Vuillemin, Gabrièl Arnaud, Herbert Bourdot, A. Galzin, Narcisse Patouillard, Julien Costantin, Henri Romagnesi, Robert Kühner, Roger Heim, André Maublanc, P. Konrad are among the many scholars who have brought honor to France. For many decades the *Bulletin de la Société Mycologique de France,* supplemented more recently by the *Revue de Mycologie* and many other periodicals, has published the contributions of these and other mycologists.

It was to be expected that Germany and the other German-speaking lands of Central Europe would have many students of systematic mycology, although the impetus of De Bary's researches and teaching was strongly in the direction of anatomy and life history of fungi. In the early days of the hundred-year period under consideration we find the names of Rabenhorst, Fuckel, and Fresenius among these systematists. These were followed by Josef Schroeter, Gustav Lindau, Georg Winter, Eduard Fischer, Walter Migula, Andreas Allescher, Heinrich Rehm, Paul Hennings, Paul and H. Sydow, Ernst Gäuman, and a host of others. Four rather recent publications in the German language contributed greatly to the furtherance of the work in systematic mycology: Engler and Prantl, *Die natürlichen Pflanzenfamilien* (1887–1938), Rabenhorst, *Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz* (1884–1938), Schroeter, "Die Pilze Schlesiens" *in* Cohn, *Kryptogamen-Flora von Schlesien* and the great *Kryptogamen-Flora der Mark Brandenburg* by Lindau and others (1905–1938). Many of the mycologists listed above participated in the preparation of various portions of these works.

Centers of Mycological Work

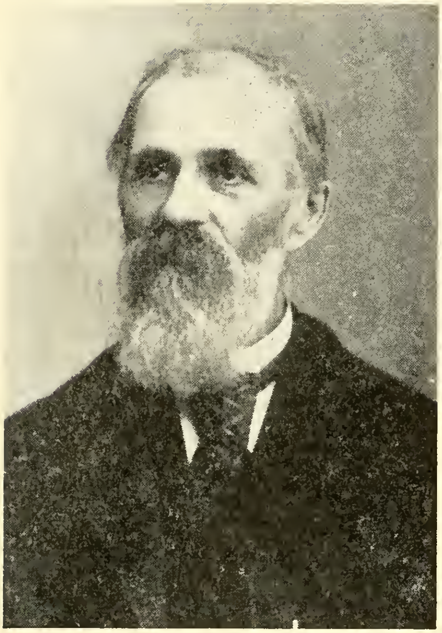
In Italy the systematic study of fungi began very actively about one hundred years ago and has continued up to the present. In the first decade of the present century we find that Dörfler's *Botaniker Adressbuch* (1909) lists 307 Italian botanists, of whom 29 were noted as interested in mycology and 13 more in plant pathology. The outstanding student in this field was Pier' Andrea Saccardo (b. 1845, d. 1920). For a large portion of his active mycological career he was Professor of Botany at the University of Padua. He became interested in the fungi in the early seventies of the last century. He established the journal *Michelia* in 1876 and continued its publication until 1882, when the great burden of writing the *Sylloge* caused him to cease publishing it. In *Michelia* appeared very many of Saccardo's first mycological contributions. Early in his mycological work he recognized that the descriptions of the fungi collected in all parts of the world were scattered far and wide, in all sorts of publications, such as local floras, monographs of genera, individual descriptions in various scientific periodicals, or even in agricultural or horticultural journals. For example, many of Berkeley's new species were described in Gardener's *Chronicle.* Furthermore, these descriptions were in various languages—Latin, Italian, German, French, English and others. Some were very brief, some very long drawn out. Thus it was impossible, unless a very extensive library was easily accessible and the various languages were not serious barriers, to be sure of the identification of a fungus. After consulting with various other mycologists, and with their encouragement and assistance, Saccardo entered (1882) upon the noted series of volumes entitled *Sylloge Fungorum*. In this *magnum opus* he attempted to bring together in systematic order all the published descriptions of fungi. Each description was in Latin and in a standard form, with the essential characters, including measurements, locality where found, etc. The work was planned to reach completion with Volume 8, which appeared in 1889, but the immense number of new species described in the meantime made it necessary to publish supplementary volumes. In the preparation of these later volumes, especially, he was assisted by various other mycologists, including his son-in-law, Alessandro Trotter; his son, Domenico Saccardo; Giovanni Battista Traverso, Paul Sydow, and others. The last volume to appear (in 1931) was Volume 25, which brought up to date, as well as the disruption of World War I and succeeding events permitted, all descriptions of fungi through 1920. It should be noted that the appearance of Volumes 22 to 25 was made possible in part by the active cooperation of Dr. W. G. Farlow, who interested various individuals and societies in America in making available a considerable sum of money, to which Dr. Farlow contributed. Since 1931, when Volume 25 finally appeared, the economic and political conditions have been such that it does not seem probable that further volumes will appear, at least not for many years.

The consequence of the publication of the first and succeeding volumes of the *Sylloge Fungorum* was a tremendous upsurge in the description of new species whose authors had hesitated to describe them for fear of adding new names to species already described. Now it became possible for an investigator working far from an extensive library to venture to describe new fungi if his volumes of the *Sylloge* did not contain their descriptions. It must be admitted that not all mycologists were as modest as indicated above and that some of these kept rushing into print with "new species," regardless of the *Sylloge*.

Because mycologists should at least know the names of new species and genera described since 1920 (i.e., after the publication of the last volume of the *Sylloge*) the Commonwealth Mycological Institute at Kew, England, has published, under the title *Index of Fungi*, lists of all such new species and genera or combinations from the year 1940 on. They have also collaborated in making available similar lists, prepared by Franz Petrak, for 1929 and 1932 to 1939. He is now working on material to fill in all the years from 1920 to 1940. Although these lists do not contain the descriptions of these new fungi, they cite the place of publication so that mycologists may avoid duplication of names as well as know where to look for new species in genera in which they are interested.

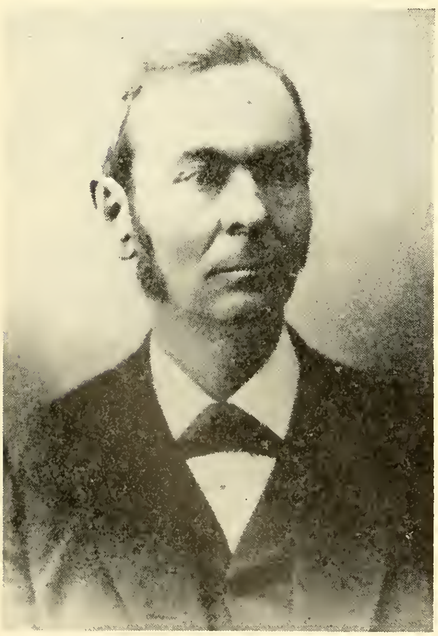
Saccardo is most widely known through the *Sylloge Fungorum*, but he was also the author of more than 140 lesser mycological contributions, including 14 numbers of *Fungi veneti novi vel critici*, from 1873 to 1882, and many numbers of miscellaneous contributions. His sporological systems of the Fungi Imperfecti (1880) and of the Pyrenomycetes (1876) exhibit the foundations upon which he based his classification of these groups.

Aside from Saccardo and his collaborators in the preparation of the *Sylloge* there are many other Italians who stand high in their profession. Augusto Napoleone Berlese is best known for his *Icones Fungorum* (1884–1905), but is the

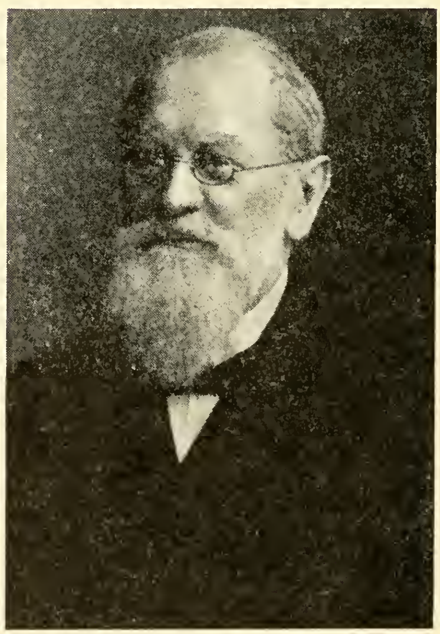


JOB BICKNELL ELLIS
1829–1905

WILLIAM GILSON FARLOW
1844–1919



CHARLES HORTON PECK
1833–1917



NATHANIEL PRINGSHEIM
1833–1894

author of many lesser contributions and of the more than 300-page monograph of the Peronosporaceae (1903), with many beautiful and accurate illustrations. Giovanni Battista Traverso was one of the leaders in the publication by the Società Botanica Italica of the work *Flora Italica Cryptogama* (I, Fungi; III, Lichens) (1905–1938). Giovanni Bresadola lived most of his life in Trentino, while it was still in Austria, but he was an Italian by descent. His *Iconographia Mycologica* (1927–1932), one of the outstanding works for the fungi of southern Europe, was published in Milan by the Società Botanica Italica. His *Fungi Tridentini* was published (1881, 1892) in Trieste. Other Italian mycologists are Teodoro Ferraris and Raffaele Ciferri.

Carlos Luis Spegazzini (b. 1858, d. 1926), of Italian nativity, settled in Buenos Aires and for several decades described hundreds of new species and a good many new genera of fungi. It may well be said that his work was the foundation upon which the knowledge of the rich mycological flora of Argentina and adjacent lands was founded. In such a vast country as Brazil with its varied climates, soils, and altitudes very much study still remains to be done on the systematic mycology of the republic. Professor Camillo Torrend published (1920–1935) a series of studies on the Polyporaceae of Brazil. Father Johann Rick, for many years a resident of the southernmost state of that country, Rio Grande do Sul, collected and studied the fungi. His interest was mainly in the Discomycetes, the larger Sphaeriales, the Thelephoraceae, and the Polyporaceae (Rick, 1931–1936). The studies of the Brazilian fungi are now being published by Ahmes Pinta Viegas and A. Ribeiro Texeira, chiefly in the periodical *Bragantia*. For Venezuela and adjacent areas, aside from the studies by mycologists from the United States and Germany, the most extensive publication is that by Chardon and Toro (1934).

In Africa the main published work on systematic mycology in recent years in the Union of South Africa is that by Ethel M. Doidge of Pretoria and by P. A. van der Byl and Len Verwoerd of the University of Stellenbosch. From Uganda in the center of equatorial Africa we have extensive lists of fungi, including many new species, from the pen of C. G. Hansford, based upon extensive collections and studies made by him during his residence there. On the whole, however, the vast continent of Africa presents a mycological void. The Italians have published some lists of fungi collected by them from Eritrea and Italian Somaliland; and from Egypt Melchers (1931) published a check list of plant diseases and fungi, but that is from a rather limited area.

In Asia the regions where active work in the study of the mycological flora has been carried on have been rather limited. In Japan, and more recently in China, in Ceylon, India, the East Indian islands, and the Philippines much has been done but very much more remains to be accomplished. The Russians have carried on quite extensive mycological explorations in Siberia and Russian central Asia, but that is so vast an area with such extremes of climate and vegetation that only a good beginning has so far been accomplished. The drier areas of southwestern Asia naturally have fewer fungi, but in the more humid valleys separated by broad desert areas one would expect a high occurrence of endemism. A little work has been done by botanical explorers in Iran, and at present the botanists of Israeli and of Turkey are active, but they have as yet barely scratched the surface. The enormous high mass of Tibet, Afghanistan, Chinese Turkestan, and the western and southwestern portions of China still await mycological study. Little has been done in Burma or the northern parts of Malaya and Indochina. The Arabian peninsula is almost untouched mycologically. It is perhaps safe to say that there will not be many new mycological discoveries made there until conditions of life and travel are safer.

The fungi of the British possessions of Ceylon and India were mostly studied by scientists sent out from Great Britain for considerable periods of time or by men like Berkeley, who remained in England and studied collections made by travelers in those regions. Dr. Edwin John Butler was the Imperial Mycologist in India from 1905–1919, returning to England to become the Director of the Imperial Mycological Institute. He published an important paper on the genus *Pythium* (1907), several papers on various rusts in India, and was a collaborator with H. and P. Sydow in a series of five numbers entitled *Fungi Indiae Orientalis* (1906–1916). With collaboration of G. R. Bisby he published *Fungi of India* (Butler and Bisby, 1931). In the last two or three decades there has been a great upsurge in mycological publications of good quality by students of Indian birth, among whom should be mentioned S. R. Bose, M. K. Patel, M. J. Thirumalachar, B. B. Mundkur and B. N. Uppal.

In Ceylon Marshall Ward studied the disease of coffee caused by the rust *Hemileia vastatrix* B. & Br. After his return to England he was succeeded by Thomas Petch, who remained in Ceylon a good many years. He studied the fungus flora very intensively. His report, published in collaboration with G. R. Bisby (Petch and Bisby, 1950), lists 2,214 species of fungi from Ceylon.

For a great many years the Botanical Garden at Buitenzorg, Java, has been a center of botanical research in almost every field of botany. Among the publications issued there have been a good many mycological papers. The occupation of Java by the Japanese, the subsequent fighting for the recovery of the island, and then the revolution which resulted in the establishment of a republic have greatly interrupted the botanical work, although the Japanese did not harm the research laboratories. Dr. K. B. Boedijn has survived these disturbances and is still doing some mycological research. The chief periodicals in which the mycological papers from Java are found are *Annales du Jardin Botanique de Buitenzorg, Bulletin du Jardin Botanique de Buitenzorg,* and *Reinwardtia.*

It has been in Japan that the chief mycological work in Asia has been carried on. For the Phycomycetes may be mentioned the work of Yosio Tokunaga on the Chytrids (1933–1934); Hiroharo Indoh on the Blastocladiaceae (1940) and Leptomitaceae (1939); Masaji Nagai on Saprolegniaceae (1931, 1933); J. Hanzawa (1915), Yoshihiko Yamamoto (1930) and Momoji Yamazaki (1934) on the genus *Rhizopus.* Sanshi Imai published papers on the Helvellaceae (1932), on the Japanese Geoglossaceae (1934–1942), on the Clavariaceae (1929–1941) and on the Agaricaceae (1933). There have been extensive studies of the Uredinales, especially the series of papers by Naohide Hiratsuka (1927 to 1939). Seiya Ito (1909 to 1922) has also published accounts of the fungi of this group.

In recent years a few Chinese botanists, of whom F. L. Tai and Lee Ling may be mentioned, have been publishing the results of their studies upon fungi collected in China. The disturbed political and economic conditions in that great country in the last twenty-five years have been very discouraging to mycological work. This may also be said of mycological work in the Philippines, where considerable work was done by American and European botanists, aided by very able students of Philippine birth; but the occupation of the islands by the Japanese in 1941 and the destruction of the centers of research put an end for many years to mycological studies.

The situation has been much brighter in Australasia. The last four decades have seen the publication of some excellent contributions to the knowledge of the smuts, rusts, Polyporaceae, and Gasteromycetes of New Zealand by G. H. Cunningham (1924 to 1950) as well as of the Polyporaceae and Gasteromycetes of Australia, by the same author (1944, 1950). Daniel McAlpine published a book on the fungi of Australia (1895) and one book each on the rusts (1906) and smuts (1910) of Australia. On the larger woody and fleshy fungi John Burton Cleland published a number of contributions, some alone (1934–1935) and some with the collaboration of Edwin Cheel (1914–1931) or of Leonard Rodway (1928–1929). Lillian Fraser (1933–1935, 1936) and Eileen E. Fisher (1939, 1950) have studied the sooty molds and related fungi of Australia. Thus it is apparent that systematic mycology has progressed far in Australasia in some of the important groups of fungi.

Mycological Work in North America

In North America the earliest important contributions to the knowledge of the fungi of the country were made by the Reverend Lewis David von Schweinitz (b. 1780, d. 1834). He collected fungi extensively in North Carolina and in Pennsylvania and his two publications (1822, 1832) listed more than 2,000 species, many hundreds of which he described as new to science. He possessed a compound microscope, good for that period. He followed in the main the system of Fries. Accordingly the group called by him (1832) Ascomycetes included both Ascomycetes and Basidiomycetes as these terms are now used. His class Hymenomycetes included Discomycetes as well as Agaricales and Polyporales of the more recent classification.

After the death of von Schweinitz in 1834 the chief botanical interest in this country for the next thirty years or more was in the collecting and naming of the vascular plants of the West, which was rapidly being explored and settled. However, there were three botanists who maintained the interest in fungi during this period. The Reverend Moses Ashley Curtis (b. 1808, d. 1872) lived the greater part of his life in North Carolina (see Shear and Stevens, 1919). He became interested in the lichens in the late 1830's and was for years in close correspondence with Edward Tuckerman, to whom he sent many specimens with full notes. In the mid-1840's he began a correspondence with M. J. Berkeley that lasted until his death. He sent several thousand specimens of fungi to Berkeley, always with careful data. Many of them were described as new species with the authority given as "B. and C." The two published a joint contribution (1850–1854) upon the fungi in the herbarium of von Schweinitz which had come into the possession of the Philadelphia Academy of Science. Curtis exchanged specimens freely with Michener, Ravenel, and other botanists. The larger portion of his herbarium is now in the British Museum but a good many of his specimens are in the Farlow Herbarium of Harvard University. Ezra

Michener (see Shear and Stevens, 1917) was a contemporary of Curtis but lived longer (b. 1794, d. 1887). He was particularly interested in the plants of southeastern Pennsylvania and made extensive collections, especially of fungi, of which he listed some 1,200 species from Chester County. He sent many of his fungi to Berkeley, some of which the latter described as new species. Perhaps Michener's greatest contribution to mycology was his rearrangement of the herbarium of von Schweinitz which was deposited in the Philadelphia Academy of Science, but in a sadly neglected condition. His own mycological collection is now in the Mycological Herbarium of the United States Department of Agriculture. The third of these almost contemporaneous amateur mycologists was Henry W. Ravenel (b. 1814, d. 1887). He was born and lived most of his life in South Carolina. He collected enthusiastically, especially lichens, which he sent to Tuckerman, and fungi, of which he sent large numbers to Berkeley, who described many new species with the tag "B. & Rav." He published little on fungi but issued five centuries of *Fungi Caroliniani Exsiccati* between 1853 and 1860. Between 1878 and 1882, in collaboration with M. C. Cooke, he issued eight centuries of *Fungi Americani Exsicatti.*

Another somewhat later botanist who developed great interest in fungi was Charles Horton Peck (b. 1833, d. 1917) who became the botanist of the New York State Museum at Albany, a position he occupied from 1867–1915. He wrote a series of *Reports of the State Botanist* from 1871 to 1913, including descriptions of numerous species of fungi, chiefly Agarics, with many colored illustrations. Many of the fungi described were new to science. Owing to the fact that he had to depend upon the descriptions, often very meager, of the European fungi and never had the opportunity to study their type specimens or the species growing wild in their type localities it is not to be wondered at that some of his identifications were erroneous. Sometimes he applied the name of a European species to a fungus that was really an American one, or the name he gave to a supposedly new species was in error because the species already had a name in Europe. In spite of these mistakes, unavoidable under the circumstances, the result of his forty-odd years of study of American fungi was the description and naming and preserving in the New York State Herbarium of numerous fungi. This collection has been available for study and reference to the later mycologists, who could thus verify their own work. Peck's work and collections have aided and inspired many mycologists, among whom may be mentioned George Francis Atkinson (b. 1854, d. 1918), Calvin Henry Kauffman (b. 1869, d. 1931), Andrew Price Morgan (b. 1836, d. 1907), William Alphonso Murrill (b. 1869), Alexander Hanchett Smith (b. 1904) and many more.

Atkinson was a member of the Botanical Department of Cornell University from 1892 to 1918. His interests were broad. In systematic mycology, he worked in his later years mostly upon the Agaricaceae, especially the genus *Amanita.* As a teacher he led many graduate students into the field of mycology.

Kauffmann was connected with the Botanical Department of the University of Michigan from 1904 until his death in 1931. He published many papers, chiefly on Agaricaceae, including monographs of the United States species of the genera *Armillaria* (1923), *Inocybe* (1924), *Gomphidius* (1925a), *Lepiota* (1925b), and *Clitocybe* (1926). His *magnum opus* was the Agaricaceae of Michigan (1918). Among the many mycologists who were at one time for longer or shorter periods his students were A. H. Smith, Edwin Butterworth Mains, Marion Lee Lohman, Delbert Swartz, Bessie Bernice Kanouse, Adelia McCrea, Dow Vawter Baxter, Lee Bonar, Frank Boyd Cotner, Lewis Edgar Wehmeyer.

William A. Murrill worked at the New York Botanical garden from 1904 to 1924, as assistant curator and curator of the mycological herbarium. He was the instigator, and from its first number until 1924 the editor, of *Mycologia,* which was the successor to, but not connected with, the *Journal of Mycology.* The *Journal* ceased publication upon the death of Professor W. A. Kellerman, its editor. In addition to his curatorial and editorial duties Dr. Murrill wrote many articles for *Mycologia* and for other journals, mostly upon the Polyporaceae and Agaricaceae. He also wrote several local floras of the Agaricaceae (1912, 1911–1918). He wrote most of Volume 9 and part of Volume 10 of the *North American Flora* (1907–1916) including most of the Polyporaceae and the Boletaceae and part of the Agaricaceae. In addition he wrote upon the resupinate Polyporaceae (1920–1921, 1942). Since his retirement from the New York Botanical Garden he has carried on mycological studies for a number of years on the Agaricaceae and Boletaceae of Florida, in affiliation with the Herbarium of the University of Florida. Murrill aroused much criticism because of his breaking away from the Friesian tradition of generic limits, especially in the Polyporaceae, following in part the suggestions of P. A. Karsten (1879, 1882), in dividing the bulky genera into numerous smaller, more compact ones based upon color and various anatomical and chemical characters that Fries did not consider important enough to warrant making generic distinctions. It is true that not all Murrill's ideas have been universally adopted, but some modern mycologists such as Singer (1949), Bondarzew (Bondarzew and Singer, 1941), William Bridge Cooke (1940), A. H. Smith (1938) go even further; in the writer's opinion, correctly.

The more conservative systematic mycologists for the greater part of a century, out of their great respect for Fries, did not venture to divide the single large genus *Agaricus* into smaller genera until Fries, himself, began to make this division. Lucien Quélet, in France (1872–1875), first used most of the Friesian subgenera as genera and Karsten (1879, 1882), following in the same line, added a good many more. As a result of the work of these mycologists and of others, between 240 and 250 genera of Agarics are now well defined, though not yet fully acknowledged. From the Friesian genus *Polyporus* have been produced in much the same way 40 to 60 genera. M. A. Donk of the Netherlands has followed along these lines in his studies of the Hymenomycetes of that country, bringing the nomenclature up to date (1928, 1931, 1933).

Two names that have become established in connection with systematic mycology in the United States are those of Job Bicknell Ellis (b. 1829, d. 1905) and Benjamin Matlack Everhart (b. 1818, d. 1904); we find the familiar E. & E. appended to descriptions of hundreds of new species. Ellis became interested in fungi by entering into correspondence with Ravenel, a correspondence which continued until the latter's death. Ellis' earlier collections of fungi, beginning about 1870, were sent partly to Berkeley and partly to Cooke and a large number of species are accordingly tagged B. & E. and C. & E. As his knowledge of fungi increased, he began describing new species independently. In 1875 he began the distribution of centuries of exsiccati entitled *North American Fungi* of which twenty-five centuries were prepared, these being followed by *Fungi Columbiani.* In 1880 he became associated in his mycological work with the well-to-do amateur botanist, Everhart, with whom he published many articles and described hundreds of new fungi. In 1892 they published jointly a very fine book which is still of great value, *The North American Pyrenomycetes,* with excellent illustrations by F. W. Anderson. In 1886, in conjunction with William Ashbrook Kellerman (b. 1850, d. 1908), Ellis and Everhart founded the *Journal of Mycology,* in which numerous articles of systematic mycological interest appeared, mainly under the authorship of the founders, singly or collectively. In 1889 this journal was taken over by the Section of Vegetable Pathology of the United States Department of Agriculture, which published it quarterly for three volumes until 1894. Then, after eight years of suspension, Dr. Kellerman took over the task in 1902, beginning with Volume 8 and continuing until the close of Volume 13, when his death put an end to the publication.

Centers of Advance

A student of the history of any science soon notices that the progress of the subject is not an even one geographically but that the centers of advance are scattered here or there. Closer examination reveals that these locations are determined by the residence at those places of some one man or group of men who are enthusiastically studying and teaching the subject. Thus in Sweden many able students gathered around Linnaeus two hundred years ago. Eighty years later Fries had many followers. Around De Bary from 1853 until his death in 1888 there was always a group of zealous students. Farlow at Harvard seventy-five years ago began to attract men in the same way, and following him were Thaxter, Weston, and White, not to mention the many students trained there and going elsewhere to form centers of their own. This sort of propagation from old center to new centers is of course only possible to any considerable extent when the scholars at the centers are associated with colleges or universites. So men like von Schweinitz, Curtis, Ravenel, Michener, and Ellis, although performing great amounts of excellent mycological work, could not propagate the spirit so widely as the men at Harvard, Cornell, Michigan, and other institutions. Coker and Couch form a mycological center at the University of North Carolina from which a good many mycologists have gone out. At Purdue University the influence of Joseph Charles Arthur built up a group, scattered among various other institutions, of specialists in uredinology. At the University of Minnesota, under the influence of Edward Morse Freeman and Elvin C. Stakman, there are gathered men studying the various races of cereal rusts in their relation to their hosts and experimenting with the breeding of strains of rusts, as well as of hosts resistant to them.

Often a sharp distinction cannot be made between the mycological and phytopathological aspects of the subject. Thus in the study of the genus *Fusarium,* as carried out by Sherbakoff, Wollenweber, Hansen, Snyder, and others, the pathogenic activities of the strains under study must be considered along with the cultural and morphological characters. Thus it is that mycological work is apt to be found where there is also active phytopathological work.

In recent years a new and very important branch of mycology has developed, the study of the fungi that produces antibiotics. In my work as a plant pathologist I had occasion frequently to work with Petri-dish cultures of bacteria or of certain fungi. Occasionally my cultures were contaminated by the entrance of spores of a *Penicillium* or *Aspergillus*. Very often around such a contaminant the bacteria or fungi under culture were suppressed. I lacked the scientific curiosity to try to learn why it happened. I was not alone in my stupidity; I have talked with others who had the same experience. But there was one man, an Englishman named Alexander Fleming, who noted the destruction of the cells of a *Staphylococcus* around the contaminating colony of a species of *Penicillium*. He did not throw away the contaminated culture or cut out the invader while the colony was still small. He wanted to find out what was happening, and why. That is how penicillin was discovered. If the rest of us had been as keen as Fleming, penicillin could have been discovered decades earlier, for Nature had given us the opportunity to observe this phenomenon. Even though Fleming recognized the possible value of penicillin and tested it against various pathogenic bacteria it was not until his *Penicillium notatum* Westl. was studied by Florey and Heatley at Oxford University and sufficient penicillin was produced to permit clinical experiments on human beings that the danger was past that this observation might be dropped from sight as merely an interesting fact. But with the outbreak of World War II a cooperative project was established in the United States, in which Florey and Heatley took part. Thus, as shown by Kenneth B. Raper in his presidential address before the Mycological Society of America in 1951 (Raper, 1952), this international cooperation involved discovery of improved methods for more production of penicillin and development of improved strains of the fungus. So in the ten-year period from the beginning of this project the *monthly* production of penicillin in America, measured in "penicillin units," rose from 400,000,000 in May, 1941, to "between 23 and 33 *trillion* units" (23,000,000,000,000 and 33,000,000,000,000) ten years later. The success of this cooperative project with the product of *Penicillium notatum* started hundreds of investigators, independently and working for pharmaceutical manufacturers, to test thousands of cultures of all sorts of fungi (including Actinomycetes) and bacteria. The result is that more than three hundred antibiotics have been discovered, of which about seven are now in mass production and use. The search still goes on. The interested reader is referred to the ponderous work of Florey *et al.* (1949), in addition to this sketchy outline.

Periodicals

One hundred years ago there was not a single scientific periodical devoted solely to the publication of mycological contributions. Léveillé published most of his important papers in *Annales des Sciences Naturelles, Botanique,* the majority of De Bary's contributions appeared in *Botanische Zeitung* of which he was the editor in the later years of his life. Among other scientific journals in which mycological papers appeared were *Flora oder allgemeine Botanische Zeitung;* Pringsheim's *Jahrbücher für Wissenschaftliche Botanik; Berichte der Deutschen Botanischen Gesellschaft; Zeitschrift für Botanik; Bulletin de la Société Botanique de France, Comptes Rendus; Annals of Botany; Nature; Broteria; Nuovo Giornale Botanico Italico; Botanical Gazette; American Naturalist; Bul-*

letin of the Torrey Botanical Club; Phytopathology; Botanical Magazine, Tokyo; Canadian Journal of Research; Tijdschrift over Plantenziekten; Zeitschrift für Pflanzenkrankheiten; Svensk Botanisk Tidskrift; and the annual transactions and bulletins of scores of scientific societies, academies, and other institutions. Possibly the earliest periodical devoted solely to mycology was *Michelia,* founded by Saccardo in 1876 and terminated in 1882. The *Journal of Mycology* was founded in 1886 and continued with some interruptions for fourteen volumes, ending in 1908. *Mycologia* began in 1909 and still continues actively. *Transactions of the British Mycological Society* began about 1916, the *Review of Applied Mycology* in 1922, the *Bulletin Trimestriel de la Société Mycologique de France,* in 1895. *Revue Mycologique* began in 1879 and came to an end fifteen or twenty years later. *Revue de Mycologie* began in 1936. In Germany *Mycologisches Centralblatt* ran from 1912 to 1915, being then a casualty of World War I. *Annales Mycologici,* 1903 to 1941, was a casualty of World War II, as was *Zeitschrift für Pilzkunde,* founded in 1921. *Sydowia* was founded in 1947 as a sort of continuation of *Annales Mycologici.* In Sweden *Friesia* ran for several years until the last war.

Classification Systems

The classification of fungi has naturally undergone great changes in the past one hundred years, corresponding with the increased knowledge of their structures and life histories, on the one hand, and with the eventual general acceptance by mycologists of the hypothesis of evolution. Before the idea of evolution had gained acceptance, the degrees of relationships of plants (and animals) were based upon the greater or smaller degrees of similarity between the organisms that were being studied. The idea of "types" was proposed. These must not be confused with the nomenclatorial types of species, genera, families, etc., whose recognition is necessary to permit the application of the valid names upon these groups. In the older use of the term a "type" was an idealized organism, a sort of composite being, including the main characters of a large group of supposedly related plants or animals. Thus *Ranunculus* was the type of a whole group of Ranunculaceae, Magnoliaceae, Annonaceae, Berberidaceae, etc. These were all considered as having been created with various modifications of the type (*Ranunculus* in this case)—the greater the modifications, the less the degree of relationship. The idea was comparable to the work of an architect who draws a basic plan for a house and then modifies it in many ways so that, although the houses are basically similar, each one differs in a few or many particulars from the others. So the Creator was supposed to have formed his generalized type for a group of plants (or animals) and then, on the day of creation, to have modified this in some degree.

It must be confessed that we who believe in evolution have had to take on some of the ideas of the earlier systematists. They measured the strength of what they called "relationship" by the degree of similarity, without accepting the idea of genetic kinship. We, too, use the degree of similarity to indicate the probable (or possible) path of the evolutionary change and so to indicate the degree of "blood relationship." As more fungi are studied and their structures and life histories determined, we have become able to suggest what may have been the more primitive forms and by what routes evolution may have produced the different groups. Theoretically, now, the ideal system of classification will attempt to indicate these lines of descent (or shall we say, ascent) from the first organisms that we may call fungi. Since, however, fungi are not easily preserved as fossils, we cannot call upon the phytopaleontologists to assist us by showing what types of fungi occurred at each geological era. Therefore we have to depend upon the study of the ends of the twigs of the phylogenetic tree and by comparing these to surmise what the trunk and the main evolutionary branches probably were.

Because of the structural differences in different groups of fungi and the different chemical constitution of their cell walls, as well as differences in their life histories, some of the earlier mycologists who believed in evolution concluded that the fungi are not necessarily a single phyletic series but that evolution from algae to fungi may have occurred at several different points. The necessary consequence of the acceptance of such a hypothesis would be belief in the polyphyletic nature of the fungi we are acquainted with, in other words, these would not represent a great group of common descent. The different groups, arising from different algae, would not be interrelated, except as one traces relationship down through their various ancestral algal stocks to their common algal ancestor.

Some of the suggested alga-to-fungus relationships are as follows: origin of Chytridiales (in the wide, older use of this term) from unicellular algae, taking into consideration the existence of certain somewhat intermediate genera which are still considered as algae but which live endophytically, e.g., *Chlorochytrium, Endosphaera, Rhodochytrium*, etc. On the contrary, it has been suggested that the Chytridiales are descended by simplification from Saprolegniales. Another suggested relationship is *Vaucheria*-like algae to Saprolegniaceae, taking into consideration the occurrence of the endophytic genus *Phyllosiphon*, showing that such an intermediate step may occur in this area of relationship. From the Saprolegniales would have arisen the Peronosporales and possibly, by simplification, the Chytridiales. The suggested origin of *Monoblepharis* from *Oedogonium* is certainly erroneous, now that the structures and life histories of both have been more fully elucidated. Similarly, the supposed connection of *Mucor* and *Spirogyra* cannot be upheld. One hypothetical connection, Florideae to Ascomycetes, suggested by Sachs (1874), has so many data to support it that to this day many mycologists, including the writer, are inclined to accept the hypothesis (see Bessey, 1942).

The classifications of the pre-evolution days have undergone great modifications, Fries (1821–1832) divided the fungi into four classes.

1. Coniomycetes: sporidia naked, without receptacles. Four orders, all except part of order Entophytae corresponding to our present Fungi Imperfecti. This latter order contained also the rusts and smuts. They were not true organisms, according to Fries, but exanthemata of diseased plants.

2. Hyphomycetes: thallus floccose, the sporidia borne upon or among the hyphae. These, too, were mainly Fungi Imperfecti.

3. Gasteromycetes: the whole fungus closed, containing the sporidia in its interior. This includes the present-day Gasteromycetes, the Mucorales, the Mycetozoa, and the Pyrenomycetes.

4. Hymenomycetes: hymenium soon exposed, bearing the sporidia superficially, in the

more perfect (i.e., typical) forms the sporidia included in the asci.[1] The class included sclerotial forms (*Sclerotium*, *Erysiphe*, etc.); *Tremella; Dacrymyces;* the *Discomycetes; Solenia; Cyphella;* with the highest order the Hymenini practically the same as the present day Hymenomycetes.

Von Schweinitz (1832) follows Fries but rearranges the classes somewhat.

A. Ascomycetes: bearing the sporidia in asci[1]
  Class I. Hymenomycetes asci on an open receptacle
  Class II. Pyrenomycetes, asci within perithecia
B. Sporomycetes: bearing free sporidia, not in asci
  Class III. Gasteromycetes, sporidia free within a peridium
    Coniomycetes of Fries, sporidia without peridium
  Class IV. Hyphomycetes, sporidia borne directly on the thallus
  Class V. Gymnomycetes, sporidia borne on a sporodochium

Berkeley (1857) made a considerable change in his classification of fungi. By this time the studies of Montagne and Léveillé had shown the difference between the ascus and the basidium. The following is Berkeley's key.

Fungales
  Sporidiiferi (sporidia in sacs)
    Ascomycetes: asci formed from the fertile cells of an hymenium
    Physomycetes: fertile cells seated on threads not compacted into an hymenium
  Sporiferi (naked spores)
    Hyphomycetes: spores naked, variously seated on conspicuous threads which are rarely compacted; mostly small in proportion to the threads
    Coniomycetes: spores naked, mostly terminal, seated on inconspicuous threads, free or enclosed in a perithecium
    Gasteromycetes: spores naked. Hymenium enclosed in a peridium, seldom ruptured before maturity
    Hymenomycetes: spores naked. Hymenium free, mostly naked, or if enclosed at first, soon exposed

In the foregoing the Ascomycetes are the same as the group we now call by that name; the Physomycetes are practically identical with our Mucorales; the Hyphomycetes consist mainly of Fungi Imperfecti, but include also *Peronospora.* The Gasteromycetes include, in addition to our present-day Gasteromycetes, also the Mycetozoa; the Hymenomycetes include the Tremellales (in the wider sense), the Polyporales, and the Agaricales. The Coniomycetes include Uredinales and Ustilaginales, in addition to some of the dematioid imperfect fungi. The Saprolegniales are still included by Berkeley among the *Conferva* group of the algae, but with the doubt expressed that *Achlya* and its allied genera may be molds. In this connection it must be remembered that Nathaniel Pringsheim (1851, 1855, 1858, 1873) at first considered these fungi algae because their vegetative structures and manner of reproduction, sexual and asexual (the latter by zoospores), were in his opinion of greater weight in assigning them to a place in the algae than their lack of starch and chlorophyll. This seems to have been De Bary's opinion in his first paper on this group (1852).

The next important classification of the fungi was that by De Bary (1866) in his textbook. He divides the fungi into four orders, the lowest, the Phycomycetes, coming first as revealing their more primitive nature and relationship

1. Remember that Fries, Schweintz, and other early mycologists did not set apart the basidia from the asci.

to the siphonaceous algae. From this order radiated the Hypodermii (smuts and rusts), the Basidiomycetes and the Ascomycetes, which he places highest in the fungal series. He has no group set aside for what we call the Fungi Imperfecti. These he rather looks upon as asexual forms of Ascomycetes whose connections with the sexual stages have not been demonstrated. Eighteen years later De Bary (1884) modified this classification by establishing two series as follows.

I. Ascomycetenreihe
  1. Peronosporeen (nebst Ancylisteen und Monoblepharis)
  2. Saprolegnieen
  3. Mucorineen oder Zygomyceten
  4. Entomophthoreen
  5. Ascomyceten
  6. Uredineen

II. Von der Ascomycetenreihe divergierende oder der Stellung nach zweifelhafte Gruppen
  7. Chytridieen
  8. Protomyces und Ustilagineen
  9. Zweifelhafte Ascomyceten (Saccharomyces, etc.)
  10. Basidiomyceten

Groups 1–4, because of their near connection with the algae, are brought together under the name Phycomycetes. In category II, groups 7 and 8 are to be treated in connection with the Phycomycetes, 9 naturally with the Ascomycetes, and 10 with 6 (Uredineae).

The *Lehrbuch der Botanik* by Julius Sachs was of great influence in the development of botanical studies. This appeared in many editions and was translated into several languages. In his earlier editions he followed De Bary for the classification of the fungi. In his fourth edition (1874) he adopted a quite different arrangement. He places the plants below the group Bryophyta in the group Thallophyta. This he divides into four classes, each containing plants with chlorophyll and those without it. The main line of evolution he indicates goes upward in the chlorophyll-containing series (i.e., the algae), the chlorophyll-free organisms in each class being derived from those with chlorophyll in the same class. In other words, the fungi are polyphyletic and do not form a single phylum.

The four classes of Sachs are the following.

I. Protophyta. No sexual reproduction	
Chlorophyll-containing	*Chlorophyll-free*
Cyanophyceae	Schizomycetes (=Bacteria)
Palmellaceae (in part)	Saccharomyces
II. Zygosporeae. Sexual union of equal cells to produce a zygospore	
With chlorophyll	*Lacking chlorophyll*
Union of motile cells	
Volvocineae (Hydrodictyeae)	Myxomycetes
Conjugation of resting cells	
Conjugatae (including Diatomeae)	Zygomycetes
III. Oosporeae. Fertilization of egg to produce an oospore	
With chlorophyll	*Lacking Chlorophyll*
Sphaeroplea	
Vaucheria	Saprolegnieae Peronosporeae
Oedogonieae	
Fucaceae	

IV. Carposporeae. Sexual reproduction results in the production of a spore fruit

With chlorophyll	*Lacking chlorophyll*
Coleochaeteae	Ascomycetes (including the Lichens)
Florideae	Aecidiomycetes
Characeae	Basidiomycetes

Sachs believed that the Saprolegniales and thence the Peronosporales arose from algae closely related to *Vaucheria* with a few differences: disappearance of chlorophyll, lack of free-swimming male gametes (these being replaced by a conjugation tube from the antherid piercing to the egg), and the production of numerous simple biflagellate zoospores instead of a large compound zoospore with hundreds of pairs of flagella. The branched coenocytic vegetative structure with cellulose cell walls, the production of zoospores in terminal segments of the hyphae, and the formation of large oögones with antherids usually arising nearby are characters common to *Vaucheria* and the Saprolegniales.

The idea that Mucorales represent developments from the Conjugatae in which the chlorophyll has been lost was adopted by Sachs from Brefeld, who emphasized the similarity of the formation of the zygospores in both groups of organisms. Although the suggestion of De Bary and Sachs that the Saprolegniales are probably derived from *Vaucheria*-like algae has persisted in some quarters (Gäumann, 1949), mycologists have been led to reject the idea of the close relationship of these groups because of other factors: the type of hyphae tubular coenocytic in Mucorales, cellular with uninucleate cells, in Conjugatae; cell wall mainly of chitin in the former, of cellulose in the latter; and abundant production of asexual wind-borne spores in the former, no special asexual cells in the latter.

In the fourth class, Carposporeae, the central feature is the production of a spore fruit, i.e., a mass of cells some of which are the spores which will produce the new plant. The spore fruit in the Ascomycetes, in which sexual organs are still functional, gives rise to ascospores contained in asci, at the ends of ascogenous hyphae originating from fertilized oögones. Around these hyphae may also be present the vegetative hyphae that form the paraphyses and the main body of the perithecium or apothecium. In many of these Ascomycetes are produced nonmotile spermatia which unite with the receptive threads (trichogynes) from the oögones and thus bring about the fertilization. This is similar to what happens in the Florideae and gave rise to Sachs's suggestion of the origin of the Ascomycetes from that group. This view still persists among many mycologists (see Vuillemin, 1912, in which a very full discussion is given of the various suggested systems of classification of the fungi).

Brefeld did not accept the ideas of Sachs and rejected those of De Bary, except the origin of the Oömycetes from the Siphoneae. For him, this group does not represent true fungi. The true fungi begin with the Mucorales, which he considers to have developed from algae that produced zygospores (e.g., Conjugatae). He emphasizes that the algae retained their sexuality and evolved into the higher green plants. The primitive fungi (the Mucorales) quickly began to magnify the importance and complexity of their asexual reproduction at the expense of the sexual reproduction, which soon disappears as evolution progresses toward the higher fungi. In the main line of fungus evolution, the basic group is class Zygomycetes (the class Oömycetes, in his view, comes to a blind end). He divides this class into three series, leading to three lines of development. These are based on the asexual reproduction as follows: sporangia alone, sporangia and conidia, and conidia alone. The first group has fungi with only the fully developed sporangia, as in *Mucor, Rhizopus,* etc., or with both sporangia and sporangioles, as in *Thamnidium.* By reduction of the sporangioles to indehiscent, monosporous cells arose the conidia of the Choanephoraceae, forming the second group, in which true sporangia as well as these conidium-like sporangioles occur. Again from *Thamnidium,* by a similar reduction of the sporangioles to conidia and the complete loss of the true sporangia, came the third group of which *Chaetocladium* is characteristic.

The higher fungi, which Brefeld calls Mycomycetes, have entirely lost their sexuality. In the Ascomycetes the ascus is derived from the sporangium of some mold, like *Choanephora* and the conidia from the reduced indehiscent sporangioles. An intermediate group, the Hemiasci, is postulated, including fungi in which the sporangium, now well on its way to become an ascus, still remains with a large indefinite number of spores, the final step being the reduction of this large number of spores to a definite number, usually eight. From the completely conidial Mucorales, such as forms of the same degree of development as *Chaetocladium,* Brefeld postulates the origin of the Hemibasidii, in which the conidiophore of this fungus has been reduced to a several-celled protobasidium with an indefinite number of spores. Here are the Ustilaginaceae and Tilletiaceae. The former gives rise, with the number of spores reduced to four but with the basidium still several-celled, to the Protobasidiomycetes, including the Uredinales and *Auricularia* and *Tremella* and *Pilacre.* From the vicinity of *Tilletia,* with its one-celled promycelium or protobasidium, arose the Autobasidiomycetes, with their spore number reduced to four. F. von Tavel (1892) devotes a very interesting little book to a discussion of the fungi in the light of Brefeld's classification.

Dangeard goes a step further in separating the fungi completely from the algae, thus forming two independent series. Both are assumed to have evolved from Protozoa of the group Flagellata. The algae became plants at the point of evolution where their flagellate, chlorophyll-containing ancestors lost the power of engulfing particles of food. The fungi arose from the flagellates that lacked chlorophyll, likewise at the point where they no longer took into their cells the particles of food. Thus the fungi are a kingdom parallel to the plant kingdom, on the one hand, and to the animal kingdom, on the other. It is worthy of note that G. W. Martin (1932) makes a somewhat similar suggestion.

Wilhelm Zopf (1890) follows a classification similar in part to that of Brefeld, but places the Ascomycetes last. In these he goes from the simple forms, like *Saccharomyces, Endomyces,* Gymnoascaceae, to, at the peak, the Pezizales. He recognizes the formation of ascogones in many Ascomycetes and even the union of these in *Pyronema,* with club-shaped "pollinodia," but expresses doubt as to their real sexual function.

The classification of fungi followed in the first edition of Engler and Prantl (1897–1907) is, in its main features, the same as that of Brefeld. In the second edition (1926–1938) the main features are retained with some modifications made necessary by the cytological confirmation of the actual occurrence of sexuality in the higher fungi as well as in the Phycomycetes. Yet this fact has not had the effect that it would seem to deserve, perhaps owing to the well-known conservatism of systematists and their reluctance to make changes in the familiar classification.

So we find the monophyletic concept of the fungi strongly entrenched. To be sure, the ideas of Sachs and a number of others (as pointed out by Vuillemin, 1912), that the fungi have arisen from algae at various points, still persist. The most recent books to use the results of the recent cytological and anatomical studies in the classification are the two books by Ernst Albert Gäumann (1926, 1949).

In his later book Gäumann recognizes four classes of fungi. The first class consists of the Archimycetes. They are endophytic parasites which, in their early vegetative stages, are naked and, in some cases at least, amoeboid. Later, the whole structure, often up to that stage still uninucleate, in spite of its growth, forms a cell wall and then by multiplication of the nuclei and division of the protoplasm becomes a zoosporangium or a gametangium, within which are contained the motile naked zoospores or gametes. Of the four families recognized two, Olpidiaceae and Synchytriaceae, are usually placed in the Chytridiales, because of the posteriorly attached single flagellum. The other two families, Plasmodiophoraceae and Olpidiopsidaceae, have two anterior or lateral flagella and are usually placed respectively near the Mycetozoa and the Saprolegniales. These four divergent families are, according to Gäumann, probably to be assigned to an origin among the Flagellata.

Gäumann's second class, the Phycomycetes is acknowledged to be at least diphyletic. The first three orders (*Reihen*), Chytridiales, Blastocladiales, and Monoblepharidales are certainly related. Their zoospores (and motile gametes, where formed) have a single posterior flagellum (which is of the whiplash type, as in the first two families of the Archimycetes), and the cell wall does not typically contain cellulose. They are derived from the Flagellata. The fourth *Reihe,* the Oömycetes, has cellulose-containing walls and the motile cells, where formed, have two anterior or lateral flagella, one of the tinsel type and one of the whiplash type. The vegetative structure is a more or less branched, coenocytic hypha on which are formed rounded oögones, with one or more eggs (oöspheres) which are fertilized by conjugation tubes from antherids that arise nearby or at a distance and become attached to the oögone. The fertilized egg becomes a thick-walled oöspore. This *Reihe* is so similar in structure to the Siphoneae, especially *Vaucheria,* that Gäumann seeks its ancestry in that general group, as did Sachs, De Bary, and others. It has several families, soil or water inhabitants and strict parasites in land plants. It ends blind, as the remainder of the fungi are not considered to have derived from the Oömycetes. The fifth *Reihe* is that of the Zygomycetes, from which the higher fungi are considered to have arisen. Vegetatively they resemble the Oömycetes, in that they are branched tubular coenocytes, but their cell wall has chitin as its chief constituent. Sexual reproduction is by the union of two nearly equal and similar gametangia to form a thick-walled zygospore. Asexual reproduction is by the formation of sporangia, within which are produced the encysted spores, instead of the naked zoospores of the preceding class. These sporangia show great modifications, leading in several directions to the production of wind-borne conidia (which in most cases represent indehiscent sporangia reduced in size, with contained spores reduced to one).

The third class, Ascomycetes, is considered to have arisen from some Zygomycete in which the union of two gametangia—instead of producing a zygospore, out of which later, on germination, a stalked sporangium arises—produces immediately the sporangium, which is specialized to become the ascus. In the subclass Protascales ascogenous hyphae and spore-fruits are lacking. Here come the orders Endomycetales (= Saccharomycetales of authors) and Taphrinales. The subclass Euascomycetes includes the rest of the Ascomycetes, in which spore-fruits are built and the asci are produced on ascogenous hyphae. The basal group of the Euascomycetes is the order Plectascales, in which the ascogenous hyphae branch through the interior of the spore-fruit so that the asci are scattered throughout it. The asci and other tissues dissolve at maturity of the ascospores so that the latter lie free in the now hollow ascocarp. The ascospores are not expelled from the asci. The spore-fruit shows varying degrees of complexity, from a loose weft of hyphae among which the ascogenous hyphae creep and produce their asci (family Gymnoascaceae) to rather massive structures (e.g., Elaphomycetaceae). Sexual reproduction by union of antherids with ascogones occurs frequently. From this order branch off two series of orders, the Ascoloculares, in which the asci are formed in cavities which they dissolve out in the stromatic tissue, and the Ascohymeniales, in which these cavities are formed during the growth of the spore fruit and then become lined by a palisade of asci. The former group includes among other orders the Perisporiales, Myriangiales, Pseudosphaeriales. In the Ascohymeniales are found the Sphaeriales (including Hypocreales), Pezizales (= the operculate Discomycetes), Helotiales (inoperculate Discomycetes) and Tuberales. The Laboulbeniales are placed at the close of the class with uncertain position as regards relationship.

The fourth class, Basidiomycetes, is placed highest because of its derivation from the higher Ascomycetes (probably some of the Discomycetes). The basidium is looked upon by Gäumann as an ascus from which have emerged four exogenous pockets containing each a single ascospore. This ascospore with its containing wall is the so-called basidiospore. Gäumann recognizes two subclasses: Holobasidiomycetes, with one-celled basidium, and Phragmobasidiomycetes, with the basidium longitudinally or transversely septate. The Holobasidiomycetes he considers the more primitive type, derived from the Ascomycetes in which the hook or crozier (or its derived form, clamp-connections) is present. The Holobasidiomycetes are divided into the Hymenomycetes, in which the basidiospores are violently expelled, and the Gastromycetes, in which the basidiospores are passively distributed.

In the second subclass, Phragmobasidiomycetes, the basidiospores are violently shot away in most of the species except in Family Ustilaginaceae. The following four groups are placed here: Tremellales, Auriculariales, Uredinales, and Ustilaginales.

The late Herbert Spencer Jackson, for many years a student of the Uredinales, published a memoir (1931) in which he compared the life cycles of the rusts with those of the red seaweeds, suggesting that the similarities might indicate relationship between these groups.

The spermogonium of the Uredinales may be considered to show relationship of the rusts to those Ascomycetes in which such structures occur.

The ideas of relationship which the author has inherited and developed in the last half-century (see Bessey, 1942, 1950) may be outlined here.

The Mycetozoa (Myxogastrales, Acrasiales, Labyrinthulales, and Plasmodiophorales) are, following De Bary, placed outside the vegetable kingdom, being considered as derived from Protozoa of the group Rhizopoda and not progressing further to produce recognized fungus groups. When the flagella of the motile cells have been examined, they are found to occur in pairs, both of the whiplash type, thus barring any connection of the Plasmodiophorales with the Olpidiopsidaceae, where one of the flagella is of the tinsel[2] type and the other of the whiplash type. The true fungi are believed to begin with the Phycomycetes. The simplest of these fall into three series: Chytridiales, with a single posterior, whiplash type flagellum; Hyphochytriales, with a single anterior flagellum of the tinsel type; and Lagenidiales (including Woroninaceae and Olpidiopsidaceae, but not the Plasmodiophoraceae) with two anterior or lateral flagella, one of the tinsel type, the other of the whiplash type. The Chytridiales connect directly with the Blastocladiales and Monoblepharidales, this line then ending blind; the Hyphochytriales have no recognized further development; the Lagenidiales lead onward to the Saprolegniales and Peronosporales. Two paths of evolution of the Chytridiales, Hyphochytriales, and of the simpler Lagenidiales are suggested. They may be primitively simple, derived from some algal ancestors of the group of Heterokostae, in which the flagella are of the two types. By the loss of the tinsel type flagellum the Chytrid type may have originated; by loss of the whiplash flagellum the Hyphochytrial group might have developed; while the Lagenidiales line may have had its beginning with the retention of both types of flagellum. But, contrariwise, these simple forms may have arisen by *simplification* from some fungi of the Lagenidiales, Saprolegniales, Peronosporales lines which, as suggested by De Bary, Sachs, Gäumann, and others may have arisen from algae in the vicinity of *Vaucheria.*

The author seeks the origin of the Mucorales in the soil-inhabiting Saprolegniales in which the sporangia produce encysted spores (as in *Aplanes*) instead of the zoospores usually found in that order. The approximately equal gametangia, such as unite to form the zygospore in *Mucor* may be a much derived form, for there are a number of genera in the Mucorales (e.g., *Dicranophora* and *Zygorhynchus*) in which the two uniting gametangia are very unequal in size and appearance, more like the antherid and oögone in some of the Saprolegniales. Akin to the Mucorales are probably the Entomophthorales and the Zoopagales. In the author's opinion, the Phycomycete line comes to an end there, not proceeding to the higher fungi.

The Ascomycetes are believed to have arisen from some algal ancestor related to the Florideae. In this algal group the oögone (carpogone) consists of a swollen basal portion with a receptive trichogyne to which a naked spermatium adheres. From the basal portion then grow out hyphae, at whose extremities are produced the carpospores or, in *Liagora tetrasporifera,* tetrasporangia. This structure of carpogone, threads, and spores is a spore-fruit with, usually, surrounding and protecting vegetative cells. In many of the Ascomycetes occur

2. The terms tinsel flagellum and whiplash flagellum were used by Couch (1941) in the sense that Vlk (1938) used the words *Flimmergeissel* and *Peitschengeissel.* They designate respectively the more slender, wavy flagellum with numerous fine lateral threads and the thicker, stiffer flagellum of two parts—a thick basal portion and, at its upper end, a thin lash. These fine details can be observed only by special staining methods or by observation with the dark-field microscope.

similar oögones with trichogynes and antherids producing nonmotile spermatia. From the fertilized oögone branch out the ascogenous hyphae at whose tips are produced the asci. This cluster of hyphae, with or without additional vegetative hyphae, is the spore-fruit. The septa of the filaments of Florideae and of the Ascomycetes are centrally perforate. If this suggested phylogeny is correct, those groups of Ascomycetes should be considered nearest the ancestral seaweeds in which oögones with trichogynes and antherids with nonmotile spermatia are to be found. This is so in the Laboulbeniales, the lichens, many of the Pezizales, Sphaeriales, etc. These are accordingly placed first in this class and the Aspergillales (Plestascales of Gäuman and many other authors) and the Saccharomycetales (Endomycetales) should be considered as developed forms. In other words, the Ascomycetes as arranged by Gäuman, stand, as it were, on their heads, with no connection indicated with the Phycomycetes.

The Basidiomycetes are considered to have arisen from the Ascomycetes, with the spores formed internally, not in the main body of the basidium (= ascus) but in external pockets. The arrangement of groups is subclass Teliosporeae (= Uredinales + Ustilaginales), Heterobasidiae (= Phragmobasidiomycetes of Gäumann) and Eubasidiae (= Holobasidiomycetes). Since these are all believed to have diverged from a more or less common Ascomycetous (Discomycete) ancestor, the immediate order in which they follow is not very important. The Uredinales of the Teliosporeae have spermogonia and receptive hyphae to which the sperm cells become attached and therefore seem to have preserved some of the features of the more primitive Ascomycetes. In the Heterobasidiae the monocaryon type of mycelium produces spermatiumlike cells which "diploidize" the monocaryon hyphae of the opposite sexual phase. This seems to retain, then, this spermatial feature of the Ascomycetous-Florideal ancestors. This even persists in some of the Eubasidiae.

So we see that, depending upon our knowledge of the structures and ontogenous development of the fungi, we can still develop systems of classification differing greatly, depending upon our own interpretation of the importance of the similarities between groups. The ultimate correct classification of the fungi has certainly not yet been devised.

LITERATURE CITED

Bary, Anton de

1852. Beitrag zur Kenntnis der *Achlya prolifera*. Bot. Zeit., 10:473–479, 489–496, 505–511, 7 pls.

1853. Untersuchungen über die Brandpilze und die durch sie verursachten Krankheiten der Pflanzen mit Rücksicht auf das Getreide und andere Nutzpflanzen. Berlin: G. W. F. Müller.

1854. Ueber die Entwickelung und den Zusammenhang von *Aspergillus glaucus* und *Eurotium*. Bot. Zeit., 12:423–434, 441–451, 465–471, 11 pls.

1858. Ueber die Myxomycetes. Bot. Zeit., 16:357–358, 361–364, 365–369.

1859. Die Mycetozoen. Ein Beitrag zur Kenntnis der niedersten Tiere. Zeitschr. Wiss. Zool., Bd. 10.

1862. Die neueren Arbeiten über die Schleimpilze und ihre Stellung im System. Flora, 45:262, 282, 301.

1863. Recherches sur le développement de quelques champignons parasites. Mémoire

BARY, ANTON DE (Cont.)

pour servir de supplément aux travaux sur la question des générations dites spontanées. Ann. Sci. Nat. Bot., sér. 4, pp. 5–148, 13 pls.

1865. Neue Untersuchungen über die Uredineen, insbesondere die Entwicklung der Puccinia graminis und den Zusammenhang derselben mit Aecidium Berberidis, Monatsber. K. Preuss. Akad. Wiss. Berlin, pp. 15–45, 1 pl.

1866. Morphologie und Physiologie der Pilze, Flechten und Myxomyceten. *In* W. Hofmeister, Handbuch der physiologischen Botanik. Bd. II. 316 pp., 1 pl., 101 figs. Leipzig: W. Engelmann.

1884. Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bacterien. 558 pp., 198 figs. Leipzig: W. Engelmann.

BARY, ANTON DE, and M. WORONIN

1870. Beiträge zur Morphologie und Physiologie der Pilze. Dritte Reihe. *Eurotium, Erysiphe, Cicinnobolus*, nebst Bemerkungen über die Geschlechtsorgane der Ascomyceten. Abh. Senckenberg. Ges. Frankfurt a. M.

BERKELEY, MILES JOSEPH

1836. British Flora, Fungi. Vol. II, pt. 2, *in* William Jackson Hooker, The British Flora. 32 + 286 pp., 15 pls. London: Longman.

1857. Introduction to Cryptogamic Botany. viii + 604 pp., 127 figs. London: H. Baillière.

1860. Outlines of British Fungology. xvii + 442 pp., 24 pls. London: Lovell Reeve.

BERKELEY, MILES JOSEPH, and M. A. CURTIS

1850–1854. Exotic fungi from the Schweinitzian herbarium, principally from Surinam. Journ. Acad. Nat. Sci. Philadelphia, n.s., 2: 277–294, 1 pl.

BERLESE, AUGUSTO NAPOLEONE

1894–1905. Icones fungorum omnium hucusque cognitorum ad usum Sylloges Saccardianae accomodatae. Padua: Publ. by author.

Besides Vols. 1, 2, and 3 devoted to Pyrenomycetes there is a Fascicula 1, on the Peronosporaceae.

1903. Saggio di una monographia delle Peronosporaceae. 316 pp., 96 figs., 4 pls. Portici: Publ. by author.

BESSEY, ERNEST ATHEARN

1942. Some problems in fungus phylogeny. Mycologia, 34:255–279, 5 figs.

1950. Morphology and Taxonomy of Fungi. xiii + 791 pp., 210 figs. Philadelphia: The Blakiston Co.

BODIN, EUGÈNE

1901. Les champignons parasites de l'homme. 208 pp., 35 figs. Paris: Masson et cie.

BONDARZEW, A., and ROLF SINGER

1941. Zur Systematik der Polyporaceen. Ann. Mycol., 39:43–65.

BREFELD, OSCAR

1872–1912. Botanische Untersuchungen über Schimmelpilze, Hefte 1–4. Leipzig: Arthur Felix.

Title changed eventually to Untersuchungen aus dem Gesammtgebiete der Mykologie, the final Heft, No. 12, in 1912. In all, over 2,500 pp., 110 pls. Hefte 1–8, Leipzig: Arthur Felix; Hefte 9–15, Münster i. W.: Heinrich Schöningh.

BRESADOLA, GIOVANNI

1881, 1892. Fungi Tridentini novi vel nondum delineati, descripti et iconibus illustrati. Vol. 1, 114 pp., 105 pls.; Vol. 2, 118 pp., 112 pls. Trieste: Publ. by author.

1927–1941. Iconographia mycologica. 27 vols., over 1380 pls. Milan: Soc. Bot. Ital.

BULLER, ARTHUR HENRY REGINALD

1909–1950. Researches on Fungi. Vols. 1–6, London: Longmans-Green and Co.; Vol. 7, Toronto: Univ. Toronto Press. In all, xciii + 3,106 pp., 9 pls., 1,145 figs.

BUTLER, EDWIN JOHN

1907. An account of the genus *Pythium* and some Chytridiaceae. Mem. Dept. Agr. India, Bot., 1:1–161, 10 pls.

BUTLER, EDWIN JOHN, and G. R. BISBY

1931. Fungi of India. Imp. Council Agr. Res. India, Sci. Monogr. No. 1, pp. xviii + 237.

CHARDON, CARLOS E., and RAFAEL S. TORO

1934. Mycological Exploration of Venezuela. Monogr. Univ. Puerto Rico, Phys. and Biol. Sci. B., Vol. 2, 353 pp., 33 pls. (1 col.), 1 map.

CLELAND, JOHN BURTON

1934–1935. Toadstools and Mushrooms and Other Larger Fungi of South Australia. 362 pp., 10 pls. (col.), 79 figs. Adelaide: Brit. Sci. Guild (Austral. Branch), Gov. Printer.

CLELAND, JOHN BURTON, and EDWIN CHEEL

1914–1916. The Hymenomycetes of New South Wales. Agr. Gaz. New South Wales, 25:507–515, 885–888, 1045–1049 (2 pls., 1 fig.); 26:325–333 (2 pls.); 27: 97–106 (2 pls.).

1918–1931. Australian fungi. Notes and descriptions. Trans. Roy. Soc. S. Australia, 42:88–138 (4 col. pls.); 43:262–315 (2 col. pls.); 47:48–78 (2 col. pls.); 48:236–252; 51:298–306; 53:217–222; 55:152–160.

CLELAND, JOHN BURTON, and LEONARD RODWAY

1928–1929. Notes on the genus *Poria*. Roy. Soc. Tasmania Pap. and Proc. (1928), pp. 31–43, 73–86; (1929), pp. 7–24.

COHN, FERDINAND

1889–1908. Kryptogamen-Flora von Schlesien. Pt. I (1889), 814 pp., Pt. II (1908), 597 pp. Breslau: Max Müller.

CONANT, NORMAN FRANCIS; DONALD STOVER MARTIN; DAVID TILLERSON SMITH; ROGER DENIO BAKER; and JASPER LAMAR CALLAWAY

1945. Manual of Clinical Mycology. 340 pp., illus. Philadelphia: W. B. Saunders Co.

COOKE, MORDECAI CUBITT

1871. Handbook of British Fungi. 2 vols. 981 pp., 7 pls., 407 figs. London and New York: Macmillan and Co.

1892. Handbook of Australian Fungi. xxxii + 457 pp. London: Williams and Norgate.

COOKE, WILLIAM BRIDGE

1940. A nomenclatorial survey of the genera of pore fungi. Lloydia, 2:81–104.

CORDA, A. C. J.

1837–1854. Icones fungorum hucusque cognitorum. 6 vols., 64 large pls. Vols. 1–4, Prague: J. G. Calve; Vols. 5–6, Prague: Fr. Ehrlich.

COUCH, JOHN N.

1941. The structure and action of the cilia in some aquatic Phycomycetes. Amer. Journ. Bot., 28:703–713, 58 figs.

CRAIGIE, JOHN HUBERT

1927a. Experiments on sex in rust fungi. Nature, 120:116–117, 1 fig.

1927b. Discovery of the function of the pycnia of the rust fungi. Nature, 120:765–767, 2 figs.

CUNNINGHAM, G. H.

1924-1930. The Ustilagineae, or smuts of New Zealand. Trans. and Proc. New Zealand Inst., 55:307–433 (7 pls.); also suppls. in Vols. 56, 57, 58, 59, 61.

1931. The Rust Fungi of New Zealand together with the Biology, Cytology and Therapeutics of the Uredinales. xx + 261 pp., 177 figs. Dunedin, New Zealand: McIndoc.

1944. The Gasteromycetes of Australia and New Zealand. xv + 236 pp., 37 pls., 1 fig. Dunedin, N. Zealand; Publ. by author.

1947–1949. New Zealand Polyporaceae, I–X. Bull. Dept. Sci. Industr. Res., New Zealand, Nos. 72–81.

1950. Australian Polyporaceae in the herbarium of the Royal Botanic Garden, Kew, and British Museum of Natural History. Proc. Linn. Soc. New South Wales, 75:3–4, 214–249, 349–350.

DANGEARD, P. A.

1907. L'origine du périthèce chez les Ascomycètes. Botaniste, 10:1–385, 91 pls.

DILLENIUS, JOHANN JACOB

1719. Catalogus plantarum sponte circe Gissam nascentium. Cum appendice, . . . 314 pp., 16 pls. Frankfurt a. M.

DONK, M. A.

1928. De Geslachten *Cantharellus*, *Craterellus* en *Dictyolus* in Nederland. Mededeel. Nederland. Mycol. Ver., 16–17:163–183.

1931. Revisie van de Nederlandse Heterobasidiomycetae (mitgez. Uredinales en Ustilaginales) en Homobasidiomycetae — Aphyllophoraceae, I. Mededeel. Nederland. Mycol. Ver., 18–20:67–200.

1933. Revision der nederländischen Homobasidiomycetae—Aphyllophoraceae, II. Med. Bot. Mus. Rijks.-Un. Utrecht (Mededeelingen van het Botanisch Museum en Herbarium van de Rijks Universiteit te Utrecht), No. 9, pp. 1–278.

DÖRFLER, I.

1909. Botaniker Adressbuch. Sammlung von Namen und Adressen der lebenden Botaniker aller Länder. 3rd rev. ed. 450 pp. Vienna: Publ. by author.

ELLIS, JOB BICKNELL, and BENJAMIN MATLACK EVERHART

1902. The North American *Pyrenomycetes*. iii + 793 pp., 41 pls. (by F. W. Anderson). Newfield, N. J.: Publ. by authors.

ENGLER, ADOLF, and KARL PRANTL

1887–1907. Die natürlichen Pflanzenfamilien. 1st ed. The parts devoted to fungi including lichens: Teil I, Abt. 1, 1*, and 1**. Leipzig: W. Engelmann.

1926–1938. *Ibid.*, 2nd ed. The parts devoted to fungi, Bd. 2, 5b, 6, 7a, 8. Leipzig: W. Engelmann.

FISHER, EILEEN E.

1939. A study of Australian "sooty moulds." Ann. Bot., n.s., 3:399–426, 1 pl., 4 figs.

1950. Some "sooty moulds" collected in Queensland. Proc. Roy. Soc. Victoria, 62: 129–135 (illus.).

FLOREY, H. W.; E. CHAIN; N. G. HEATLEY; M. A. JENNINGS; A. G. SANDERS; E. P. ABRAHAM; and M. E. FLOREY

1949. Antibiotics. 2 vols., 1,774 pp. London, New York, Toronto: Oxford Univ. Press.

FRANKEN, J. L. M.

1937. Uit die lewe van 'n beroemde Afrikaner, Christiaan Hendrik Persoon. Ann. Univ. Stellenbosch, Jaargang XV, Reeks B, Afd. 4, 102 pp. (with portrait).

FRASER, LILLIAN

1933–1935. An investigation of the sooty molds of New South Wales. Proc. Linn. Soc. New South Wales, 58:375–395; 59:123–142; 60:97–118, 159–278, 280–290. In all, 254 figs.

1936. Notes on the Trichopeltaceae and Atichiaceae in New South Wales and on their mode of nutrition, with a description of a new species of Atichia. Proc. Linn. Soc. New South Wales, 61:277–284, 4 pls., 10 figs.

FRESENIUS, JOHANN BAPTIST GEORG WOLFGANG

1850–1865. Beiträge zur Mykologie. Heft 1, 1850; Heft 6, 1852; Heft 3, 1865. Frankfurt a. M.

FRIES, ELIAS MAGNUS

1821–1832. Systema mycologicum sistens fungorum ordines, genera et species, huc usque cognitas. 3 vols, 1,866 pp. Greifswald: Ernest Mauritius.

1836–1838. Epicrisis systematis mycologici seu synopsis Hymenomycetum. xiv + 610 pp. Upsala: Typographia Academica.

FUCKEL, KARL WILHELM GOTTLIEB LEOPOLD

1869–1875. Symbolae mycologicae. Beiträge zur Kenntniss der Rheinischen Pilze (with 3 suppls., 1871, 1873, 1875). In all, 656 pp., 7 pls. Wiesbaden: Julius Niedner.

GÄUMANN, ERNST ALBERT

1926. Vergleichende Morphologie der Pilze. 626 pp., 398 figs. Jena: G. Fischer. Eng. trans. by Carroll William Dodge, 1928. New York: McGraw Hill Co.

1949. Die Pilze. Grundzüge ihrer Entwicklungsgeschichte und Morphologie. 382 pp., 440 figs. Basel: Verlag Birkhäuser.

GUÉGUEN, FERNAND

1904. Les champignons parasites de l'homme et des animaux. Preface by M. Maxine Radais. xvii + 299 pp., 12 pls. Paris: Maison d'éditions, A. Joanin et cie.

HAGELSTEIN, ROBERT

1944. The Mycetozoa of North America, Based upon the Specimens in the New York Botanical Garden. 306 pp., 16 pls. Mineola, N. Y.: Publ. by author.

HANZAWA, JUN.

1915. Studien über einige *Rhizopus*-Arten. Mycol. Centr., 5:230–246, 257–281, 12 figs.

HARPER, ROBERT ALMER

1896. Ueber das Verhalten der Kerne bei der Fruchtentwickelung einiger Ascomyceten. Jahrb. Wiss. Bot., 29:655–685, 2 pls.

HIRATSUKA, NAOHIDE

1927. Beiträge zu einer Monographie der Gattung *Pucciniastrum* Otth. Journ. Fac. Agr. Hokkaido Imp. Univ., 21:63–119, 1 pl.

1929. Thekopsora of Japan. Bot. Mag. (Tokyo), 43:12–22.

1935. Phragmidium of Japan. Jap. Journ. Bot., 7:227–229, 2 pls.

1935–1936. Phakopsora of Japan. Bot. Mag. (Tokyo), 49:781–788, 853–860; 50:2–8.

1936. A monograph of the Pucciniastreae. ix + 374 pp., 11 pls. Tottori, Japan.

1936–1937. *Gymnosporangium* of Japan. Bot. Mag. (Tokyo), 50:481–488, 549–555, 593–599, 661–668 (2 pls.); 51:1–8.

IMAI, SANSHI

1929. On the fungus inhabiting Cordyceps and Elaphomyces in Japan. Trans. Sapporo Nat. Hist. Soc., 11:31–37.

1929–1941. On the Clavariaceae of Japan. I–VI. Trans. Sapporo Nat. Hist. Soc., 11:38–45, 70–77; 12:9–12; 13:377–384; 16:209–217, 244–250.

IMAI, SANSHI

1932. Contributions to the knowledge of the classification of the Helvellaceae. Bot. Mag. (Tokyo), 46:172–175.

1932–1934. Studies on the Hypocreaceae of Japan: I and II. Trans. Sapporo Nat. Hist. Soc., 12:114–118 (2 figs.); 14:101–106 (1 fig.).

1934. On a new species of *Cordyceps* parasitic on *Elaphomyces* in Japan. Proc. Imp. Acad. Japan, 10:68–74.

1934–1938. Studies on the Geoglossaceae of Japan: I–IV. I. Trans. Sapporo Nat. Hist. Soc., 13:179–184 (1 pl.); II–IV. Bot. Mag. (Tokyo), 50:9–16, 671–676; 52:417–424.

1938. Studies on the Agaricaceae of Hokkaido. Journ. Fac. Agr. Hokkaido Imp. Univ., 43:1–378, 5 pls.

1940. The Geoglossaceae of Norway. Ann. Mycol., 38:268–278, 4 figs.

1941. Geoglossaceae Japoniae. Journ. Fac. Agr. Hokkaido Imp. Univ., 45:155–264, 4 pls., 6 figs.

1942. Contributions ad studia monographica Geoglossarum. Bot. Mag. (Tokyo), 56:523–527, 3 figs.

IMPERIAL MYCOLOGICAL INSTITUTE (later, COMMONWEALTH MYCOLOGICAL INSTITUTE)

1940–1950. Index of fungi. Published 1940–1947 as Suppls. 1–15, Rev. Applied Mycol. Beginning with 1948 as Vol. I, Index of Fungi (pts. 16–20) and from 1950 onward with two parts to each annual volume.

INDOH, HIROHARO

1939, 1940. Studies on Japanese aquatic fungi: I. On *Apodachlyella completa* sp. nov., with revision of the Leptomitaceae. II. The Blastocladiaceae. Sci. Repts. Tokyo Bunrika Daigaku, B., 4:43–50, 237–384, 1 pl., 45 figs.

ITO, SEIYA

1909. On the Uredineae parasitic on the Japanese Gramineae. Journ. Coll. Agr. Tohuku Imp. Univ., Sapporo, Japan, 3:179–362, 3 pls.

1922. *Uromyces* of Japan. Journ. Coll. Agr. Hokkaido Imp. Univ., Sapporo, Japan, 11:211–287, 2 pls.

JACKSON, HERBERT SPENCER

1931. Present evolutionary tendencies and the origin of the life cycles in the Uredinales. Mem. Torrey Club, 18:1–108, 1 fig.

JOST, LUDWIG

1930. Zum hundertsten Geburtstag Anton de Barys. Zeitschr. Bot., 24:1–74 (with portrait).

KARSTEN, PETER ADOLF

1879–1882. Rysslands, Finlands, och den Skandinavska Halföns Hattsvampar. Bidr. till kännedom af Finlands Natur och Folk, 32:i–xxvii, 1–550; 37:v–xix, 1–245.

KAUFFMAN, CALVIN HENRY

1918. The Agaricaceae of Michigan. Mich. Geol. and Biol. Surv. Publ. 26 (Biol. ser. 5), 1:1–924, 4 figs.; 2:1–10, 172 pls.

1923. The genus *Armillaria* in the United States and its relationships. Pap. Mich. Acad. Sci., 2:53–67, 4 pls.

1924. *Inocybe*. *In* North American Flora, 10 (pt. 4): 227–260.

1925a. The genus *Gomphidius* in the United States. Mycologia, 17:113–126, 3 pls.

1925b. The genus *Lepiota* in the United States. Pap. Michigan Acad. Sci., 4:311–314, 2 pls.

1926. The genus *Clitocybe* in the United States, with a critical study of all north temperate species. Pap. Michigan Acad. Sci., 8:152–204, 7 pls.

KNORR, LOUIS CARL

1951. Berkeley. Observations, Botanical and Physiological, on the Potato Murrain. (Also selections from the author's Vegetable Pathology.) Phytopathol. Classics, No. 8.

KRYPTOGAMENFLORA DER MARK BRANDENBURG

1905–1938. Sections on fungi in Bd. 5, 5a, 6, 6a, 7, 9. Leipzig: Gebr. Borntraeger.

LARGE, E. C.

1940. The Advance of the Fungi. 488 pp., 6 pls., 58 figs. New York: Henry Holt.

LÉVEILLÉ, JOSEPH HENRI

1837. Recherches sur l'hyménium des champignons. Ann. Sci. Nat. Bot., sér. 2, 8:321–338.

1846. Considerations mycologiques suivies d'une nouvelle classification des champignons. 136 pp. Paris: Martinet.

1851. Organization et disposition méthodique des espèces qui composent le genre *Erysiphe*. Ann. Sci. Nat. Bot., sér. 3, 15:109–179.

1855. Iconographie des champignons de Paulet. Receuil de 217 planches dessinées d'après nature, gravées et caloriées . . . viii + 135 pp. Paris: J. B. Baillière.

LINDLEY, JOHN

1853. The Vegetable Kingdom. 3rd ed. lxviii + 918 pp., frontis., 526 figs. London: Bradley and Evans.

LINNAEUS, CAROLUS

1753. Species plantarum exhibentes plantas rite cognitas, ad genera relatas, cum differentiis specificis, nominibus trivialibus synonymis selectis, locis natalibus, secundum systema sexuale digestas. 2 vols., x + 1,200 pp. and index. Stockholm: Laurentius Salvius.

LISTER, ARTHUR

1925. A Monograph of the Mycetozoa. 3rd ed., rev. by Gulielma Lister. xxxii + 296 pp., 222 pls., 60 figs. London: Publ. by Trustees of the British Museum.

MCALPINE, DANIEL

1895. Systematic Arrangement of Australian Fungi . . . vii + 236 pp. Dept. Agri., Victoria. Melbourne: Gov. Printer.

1906. The Rusts of Australia. vii +349 pp., 55 pls., 28 figs. Melbourne: Dept. Agr., Victoria.

1910. The Smuts of Australia. vii + 288 pp., 56 pls., 15 figs. Melbourne: Dept. Agr., Victoria.

MARTIN, GEORGE WILLARD

1932. Systematic position of the slime molds and its bearing on the classification of the fungi. Bot. Gaz., 93:421–435.

1949. Fungi, Myxomycetes, Ceratiomyxales, Liceales, Trichiales, Stemonitales, Physarales. N. Amer. Flora, 1:1–190.

MASSEE, GEORGE

1892. A Monograph of the Myxogastres. 367 pp., 12 pls. London: Methuen and Co.

1892–1895. British Fungus-Flora. A Classified Text-Book of Mycology. 4 vols. In all, xii + 1,926 pp., illus. London: Duckworth and Co.

1902. European Fungus-Flora. Agaricaceae. vi + 274 pp. London: Duckworth and Co.

1910. A Text-Book of Fungi. xi + 427 pp. London: Duckworth and Co.

MELCHERS, LEO EDWARD

1931. A check list of plant diseases and fungi occurring in Egypt. Trans. Kansas Acad. Sci., 34:41–106.

MICHELI, PIER' ANTONIO

1729. Nova plantarum genera juxta Tournefortii methodum disposita . . . xxii + 234 pp., 108 pls. Florence: B. Papreinii.

MURRAY, JAMES A. H.

1908. A New English Dictionary on Historical Principles. Vol. 6. Oxford: Clarendon Press.

MURRILL, WILLIAM ALPHONSO

1910–1932. North American Flora. Polyporaceae (pars), Boletaceae, and a large part of the Agaricaceae. Vols. 9 and 10 (not complete). New York: N. Y. Bot. Gard.

1911–1918. The Agaricaceae of tropical North America. Mycologia, 3:23–36, 79–91, 189–199, 271–282; 4:72–83; 5:18–36; 10:15–33, 62–85.

1912. The Agaricaceae of the Pacific Coast. Mycologia, 4:205–217, 231–262, 294–308.

1920–1921. Light colored resupinate Polypores. Mycologia, 12:77–92, 299–308; 13: 83–100, 171–178.

1942. Florida resupinate Polypores. Mycologia, 34:595–596.

NAGAI, MASAJI

1931. Studies on the Japanese Saprolegniaceae. Journ. Fac. Agr. Hokkaido Imp. Univ., 32:1–43, 7 pls.

1933. Additional notes on the Japanese Saprolegniaceae. Bot. Mag. (Tokyo), 47: 136–137, 1 fig.

PERSOON, CHRISTIAAN HENDRIK

1801. Synopsis methodica fungorum, sistens enumerationem omnium huc usque detectarum specierum, cum brevibus descriptionibus nec non synonymis et observationibus selectis. Pts. I and II. xxx + 706 pp. and index, 5 pls. Göttingen: H. Dieterich.

1822–1828. Mycologia Europaea seu completa omnium fungorum in variis Europaeae regionibus dectectorum enumeratio, methodo naturali disposita, descriptione succincta, synonymia selecta et observationibus criticis additis. 3 secs., 9 vols., 852 pp., 80 col. pls. Erlangen: Johann Jacob Palm.

PETCH, THOMAS, and G. R. BISBY

1950. The fungi of Ceylon. Peradeniya Manual, No. VI, pp. 1–111.

PETRAK, FRANZ

1944. Verzeichnis der neuen Arten, Varietäten, Formen, Namen und wichtigsten Synonyme der Pilze, 1932–1935. Just's Bot. Jahresber., 63:805–1056.

1950. Index of fungi, 1936–1939, pp. 1–117. Commonwealth Mycol. Inst.

1952a. Index of fungi, 1929, reprint from Just's Bot. Jahresber., 57:592–631. Commonwealth Mycol. Inst.

1952b. Index of fungi, 1930, reprint from Just's Bot. Jahresber., 58:447–570.

PRINGSHEIM, NATHANIEL

1851. Die Entwickelungsgeschichte der *Achlya prolifera*. Nova Acta Leop.-Carol., 23:291–394.

1855. Ueber die Befruchtung und Vermehrung der Algen. Ann. Sci. Nat. Bot., sér. 4, 3:363–382.

1858. Beitrag zur Morphologie und Systematik der Algen. II. Die Saprolegnieen. Pringsh. Jahrb. Wiss. Bot., 1:284–306 (Taf. 19–21).

1873. Weitere Nachträge zur Morphologie und Systematik der Saprolegnieen. Pringsh. Jahrb. Wiss. Bot., 9:191–234, illus.

QUÉLET, L.

1872–1875. Champignons du Jura et des Vosges. 3 pts. Montbellard.

RABENHORST, L.

1884–1938. Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. 2nd ed. The parts devoted to fungi including lichens are Bd. 1, 8, 9. Leipzig: E. Kummer.

RAPER, KENNETH B.

1952. A decade of antibiotics in America. Mycologia, 44:1–59, 4 figs. (portrait).

RICK, JOHANN

1931–1936. Various publications on Pezizales, Sphaeriales, Thelephorales, and Polyporales. Broteria.

ROBIN, CHARLES PHILIPPE

1853. Histoire naturelle des végétaux qui croissent sur l'homme et sur les animaux vivants. 702 pp., 15 pls. Paris: J. B. Baillière.

SABOURAUD, RAIMOND

1894a. Sur une mycose innominée de l'homme, la teigne tondante spéciale de Gruby, *Microsporon Audouini.* Ann. Inst. Pasteur, 8:83–104, 4 figs.

1894b. Les trichophyties humaines, avec atlas. Paris: Rueff et cie.

1910. Maladies du cuir chevelu. III. Les maladies cryptogamiques. Les teignes. 855 pp., 28 pls., 433 figs. Paris: Masson et cie.

SACCARDO, PIER' ANDREA

1876. Conspectus generum Pyrenomycetum italicorum systemate carpologico dispositorum. Nuovo Giorn. Bot. Ital., 8:11–15.

1880. Conspectus generum fungorum Italiae inferiorum, nempe ad Sphaeropsideas, Melanconieas et Hyphomyceteas pertinentium, systemate sporologico dispositorum. Michelia, 2:1–38.

1882–1931. Sylloge fungorum omnium hucusque cognitorum. 25 vols. Pavia, Italy: Publ. by author.

SACHS, JULIUS

1874. Lehrbuch der Botanik nach dem gegenwärtigen Stand der Wissenschaft. xvi + 928 pp., 492 figs. Leipzig: W. Engelmann.

SARTORY, A.

1920. Champignons parasites de l'homme et des animaux. 895 + 47 pp., 50 pls., 91 figs. Paris: Lefrançois, ed.

1923. *Ibid.*, 1er supplément. 78 pp., 2 pls., 11 figs. Paris: Lefrançois.

1927. (With J. Bailly). 2ème suppl. 99 pp. Paris: Éditions Clinique et Laboratoire.

1933. (With A. Godeau, R. Sartory, L. Bailly, and J. Meyer). 3ème suppl. 150 pp. Paris: Éditions Clinique et Laboratoire.

SCHLEIDEN, MATTHIAS JAKOB

1850. Grundzüge der wissenschaftlichen Botanik, nebst einer methodologischen Einleitung als Anleitung zum Studium der Pflanze. 3rd rev. ed. Pt. II. xvi + 619 pp., illus. Leipzig: W. Engelmann.

SCHROETER, JOSEF

1889–1908. Die Pilze Schlesiens. *In* Ferdinand Cohn, Kryptogamen-Flora von Schlesien. Pt. I (1889), pp. 1–814; Pt. II (1908), pp. 1–597.

1889. Myxomycetes. *In* Adolf Engler and Karl Prantl, Die natürlichen Pflanzenfamilien. Pt. I, Abt. 1.

1892–1893. Phycomycetes. *Ibid.*

1894. Ascomycetes (in part). *Ibid.*

SCHWEINITZ, LEWIS DAVID VON

1822. Synopsis fungorum Carolinae superioris. D. F. Schwaegrichen, ed. Schr. Naturf. Ges. Leipzig, 1:20–131, 2 pls.

SCHWEINITZ, LEWIS DAVID VON

1832. Synopsis fungorum in America Boreali media degentium. Trans. Amer. Philos. Soc. n.s., 4:141–318, 1 pl.

SCHWENDENER, SIMON

1867. Ueber die wahre Natur der Flechten. Verh. Schweiz. Naturf. Ges. Rheinfelden, Aaran. Bd. 1867, p. 88.

1868. Ueber Beziehungen zwischen Algen und Flechtengonidien. Bot. Zeit., 26:289–292.

SHEAR, CORNELIUS LOTT, and NEIL EVERETT STEVENS

1917. The botanical work of Ezra Michener. Bull. Torrey Club, 44:547–558.

1919. The mycological work of Moses Ashley Curtis. Mycologia, 11:181–201.

SINGER, ROLF

1949. The Agaricales (mushrooms) in modern taxonomy. Lilloa Rev. Bot., 22:1–834, 29 pls.

SMITH, ALEXANDER HANCHETT

1938. Common edible and poisonous mushrooms of southeastern Michigan. Cranbrook Inst. Sci. Bull., No. 14, pp. 1–71, illus.

STEVENS, N. E., and C. L. SHEAR

1921. The correspondence of Schweinitz and Torrey. Mem. Torrey Club, 16:119–300.

SYDOW, H. and P., and E. J. BUTLER

1906–1916. Fungi Indiae Orientalis. Pts. 1–5. Ann. Mycol., 4:424–445; 5:485–515 (several figs.); 9:372–421 (1 pl., 9 figs.); 10:243–280 (11 figs.); 14:177–220 (4 figs.).

TAVEL, FRANZ VON

1892. Vergleichende Morphologie der Pilze. ii + 208 pp., 90 figs. Jena.

TEIXEIRA, A. RIBEIRO

1945–1950. Himenomicetos brasileiros. I-V. I. Bragantia, 5(1945):153–186 (14 pls.); II. *Ibid.*, pp. 397–439 (16 pls.); III. *Ibid.*, 6(1946):143–145 (8 figs.); IV. *Ibid.*, 8(1948):75–80 (5 pls.); V. *Ibid.*, 10(1950):113–122 (13 pls.).

TOKUNAGA, YOSIO

1933–1934. Studies on the aquatic Chytrids of Japan. I. Woroninaceae. II. Olpidiaceae. III. Rhizidiaceae. Trans. Sapporo Nat. Hist. Soc., 13:20–28, 78–84, 388–393, 3 pls.

1934. Notes on the Lagenidiaceae of Japan. Trans. Sapporo Nat. Hist. Soc., 13:227–232, 3 figs.

TORREND, C.

1920–1935. Les Polyporacées du Brésil. Broteria.

TRAVERSO, G. B., *et al.*

1905–1938. Flora Italica Cryptogama. I. Fungi. III. Lichenes. Publ. under the auspices of the Soc. Bot. Ital.

TULASNE, LOUIS RENÉ

1853. Note sur la germination des spores de Urédinées. Compt. Rend. Acad. Sci., 36:1093–1095.

1854. Sur le dimorphism des Urédinées. Compt. Rend. Acad. Sci., 38:761–765.

TULASNE, LOUIS RENÉ, and CHARLES TULASNE

1861–1865. Selecta fungorum carpologia. 3 vols., 782 pp., 61 pls. Paris: Typographie Imp.

UNGER, FRANZ JOSEF ANDREAS NICOLAUS

1833. Die Exanthème der Pflanzen und einige mit diesen verwandte Krankheiten der Gewächse, pathogenetisch und nosographisch dargestellt. xii + 422 pp., 7 pls. Vienna: Gerold.

VIEGAS, AHMES PINTA, and A. RIBEIRO TEIXEIRA

1943. Alguns fungos do Brasil. Phycomycetos. Bragantia, 3:223–270, 22 pls, 4 figs.

1944a. Alguns fungos do Brasil. II. Ascomicetos. Bragantia, 4:1–171, 220 pls., 54 figs.

1944b. Alguns fungos do Brasil. III. Ustilaginales. Bragantia, 4:739–751, 10 pls., 4 figs.

1945a. Gastromicetos. Bragantia, 5:583–595.

1945b. Fungi imperfecti (Sphaeropsidales). Bragantia, 5:715–780.

1946. Fungi imperfecti. Bragantia, 6:1–37, 11 pls., 6 figs.

VIRCHOW, RUDOLF

1856. Beiträge zur Lehre von den beim Menschen vorkommenden Parasiten. Virchow's Archiv., 9:557–593, 1 pl.

VLK, WLADIMIR

1938. Ueber den Bau der Geissel. Archiv. f. Protistenk., 90:448–488, 1 pl., 12 figs.

VUILLEMIN, PAUL

1912. Les champignons, essai de classification. 425 pp. Paris: Octave Doin et fils, eds.

1931. Les champignons parasites et les mycoses de l'homme. Encycl. Mycol. Vol. 2. 290 pp., 140 figs. Paris: Paul Lechevalier et fils.

WALLROTH, FRIEDRICH WILHELM

1833. Flora Cryptogamica Germaniae. Pars posterior, continens algas et fungos. lvi + 923 pp. Nürnberg: J. L. Schrag.

YAMAMOTO, YOSHIHIKO

1930. Ein Beitrag zur Kenntnis der Gattung *Rhizopus*. I. Morphologisches. Journ. Fac. Agr. Hokkaido Imp. Univ., 28:1–101, 4 pls.

YAMAZAKI, MOMOJI

1934. On the classification of *Rhizopus* species. (Jap. with Eng. summary). Bull. Utsonomiya Agr. Coll., No. 5, pp. 1–16.

ZOPF, FRIEDRICH WILHELM

1884. Zur Kenntnis der Phycomyceten. I. Zur Morphologie und Biologie der Ancylisteen and Chytridiaceen, zugleich ein Beitrag zur Phytopathologie. Nova Acta Leop., 47:141–236, 10 pls.

1890. Die Pilze in morphologischer, physiologischer, biologischer und systematischer Beziehung. xii + 500 pp., 163 figs. Breslau: E. Trewendt.

BRYOLOGY

By WILLIAM C. STEERE
Stanford University

THE LAST HUNDRED YEARS have brought substantial and noteworthy progress to the field of bryology; in fact, the century just past may appropriately be termed the golden age of systematic and floristic studies on bryophytes, since in these years the number of known species increased tenfold. This account of progress opens with especial suitability with the year 1851, because that marks the date of completion and of publication of the last attempt to bring together, in a single work, descriptions of all mosses of the whole world (C. Müller, 1848–1851). In this great work Müller described fewer than 2,400 species of Musci and only 25 species of Sphagnum. The great contemporary treatment of the world's hepatics (Gottsche, Lindenberg and Nees, 1844–1847), completed very shortly before the opening of the century under consideration here, brought together for the first time descriptions of some 1,600 species. This was the age of descriptive botany—systematic, morphologic, and anatomic. The field of plant physiology was still primitive and with little application to bryophytes. Before Darwin and Mendel such fields as phylogeny, genetics, cytogenetics, and cytotaxonomy—as well as experimental morphology and biochemical physiology—naturally did not exist.

The task of summarizing the development of the field of bryology during the past century, in all its ramifications, is by no means an easy one, because of the extensive and unorganized literature. Bryology, aside from its purely systematic and floristic aspects, has been established as a field so recently, and by so few workers, that no over-all summaries or compendia have yet been produced, with the outstanding exception of the *Manual of Bryology,* an excellent symposium edited by Verdoorn (1932). The widely scattered nature of the literature of bryology, falling rather sharply into specialized categories, makes it difficult indeed for those in other fields—and for bryologists themselves—to gain any general insight into the philosophies, the outlooks, and the problems of bryology. In the limited space available for this review, the most effective approach seems to be to outline briefly the modern developments in various aspects of bryology and to furnish key citations to relatively recent publications, through which interested persons may gain access to the fuller literature of any special topic. The selection of titles for inclusion in the Bibliography largely emphasizes recency rather than size or general importance of the contribution, since a sometimes relatively small recent paper will not only supply references to the important earlier literature but may also furnish supplementary information. Although the rigorous selection practiced here prevents the Bibliography from exceeding all bounds, it also calls for the author's apology to many bryologists whose important works have been excluded.

Because of the lack of comprehensive surveys of the literature of bryology during the past twenty years, the citations given here will supplement those of the important but somewhat specialized bibliographies published by Brotherus (1924–1925) in Engler and Prantls' *Die natürlichen Pflanzenfamilien,* by Herzog (1926) in *Geographie der Moose,* by Herzog (1925) and Lorch (1931) in Linsbauer's *Handbuch der Pflanzenanatomie,* and by various authors in Verdoorn's (1932) *Manual of Bryology.* The reader is also referred to reports of original research, reviews of publications, and lists of bryological papers, published in the several journals devoted exclusively or in large part to bryology, which will be considered first because of their broad coverage.

Journals

The appearance and subsequent growth of several journals devoted primarily to bryological research demonstrates impressively the progress of the field of bryology during the past century. In 1874, Husnot, the leading French bryologist of his time, founded the first bryological journal, *Revue Bryologique,* of which he continued as publisher and editor for fifty-three years, until 1926. Pierre Allorge revived the *Revue Bryologique* in 1928 and soon enlarged its scope to include papers on lichens, under the expanded title *Revue Bryologique et Lichénologique.* After Allorge's death in 1944 (cf. Blaringhem, 1944), his journal continued its existence under the able editorship of his widow, Mme. Valia Allorge, reaching its twenty-first volume during 1952. With the exception of the short-lived *Bryologische Zeitschrift,* of which the editor, Leopold Loeske, published a single volume (1916–1917), no German periodical has devoted itself exclusively to bryological contributions, although the eighty-one volumes of the general cryptogamic journal, *Hedwigia,* include a great number of important papers on bryophytes. In Great Britain the Moss Exchange Club, founded in 1896, became in 1922 the British Bryological Society. The twenty-seven *Annual Reports of the Moss Exchange Club* and the *Annual Reports of the British Bryological Society* published between 1923 and 1946 contain a very considerable amount of information, especially on local distribution of bryophytes in the British Isles. The *Annual Reports* of the Society were replaced in 1947 by the *Transactions of the British Bryological Society,* a valuable annual publication with greater emphasis on the results of original research than its predecessors. In the United States, the American Bryological Society publishes a quarterly journal, *The Bryologist.* Founded in 1898 as the Sullivant Chapter of the Agassiz Association by A. J. Grout and Elizabeth G. Britton, this organization became in 1899 the Sullivant Moss Society, a name retained until 1948. Grout established *The Bryologist* in 1898, for the first two years as a department of the *Fern Bulletin,* and thereafter as a separate and independent journal. With the fifty-seventh annual volume, completed in 1954, *The Bryologist* takes its place among the oldest botanical journals in the United States. The first sixteen volumes appeared under the editorship of A. J. Grout and Annie M. Smith, either jointly, or with one or the other as sole editor. In 1913, with Volume 17, O. E. Jennings undertook editorial supervision of *The Bryologist,* and served as editor-in-chief for twenty-five years. In 1938, with Volume 41, the responsibility for editing and managing *The Bryologist* passed into the hands of W. C. Steere. Two bryological journals have appeared in the Netherlands. In 1929 Frans Verdoorn established *Annales Bryologici*, a yearbook of exceptionally high quality, published for twelve years, with four supplementary volumes. In 1947 W. Meijer began the publication of an interesting mimeographed journal *Buxbaumia*, for the communications of the Bryologische Werkgroep of the Netherlands Natural History Society. In Japan, S. Hattori established the *Journal of the Hattori Botanical Laboratory* in 1947, and the several small volumes published to date seem to deal almost exclusively with bryology. The journals just described contain a large proportion of the original literature of bryology and provide access to most of the remainder, through reviews, lists of publications, and the bibliographies of individual original contributions.

Floristic Studies

As already indicated, the past century stands out as one of unparalleled botanical exploration, which resulted in bryological collections from nearly every part of the world and made possible an understanding of the larger outlines of bryogeography. Nevertheless, a very large amount of local and regional work still remains to be done in many areas, in order to clarify and formulate floristic and distributional problems. Of several bryologists studying the new and exciting floras of the world during the past century, Carl Müller was by far the most industrious and prolific in the creation of new species and genera of mosses. Perhaps half of the species of Musci described during the first fifty years of the past century bear the authorship of Müller, who, because of the reputation in exotic bryology established through his great work *Synopsis Muscorum* (1848–1851), received almost all collections made by the numerous German official expeditions and private collectors of his time. Furthermore, he held a very narrow specific and generic concept (Fleischer, 1922). Müller's last book, published posthumously (C. Müller, 1901), contains a complete bibliography of his important contributions. In the systematic and floristic study of hepatics, Franz Stephani (cf. Beauverd, 1928) appeared as the nearly exact counterpart of Müller in his willingness to study all exotic hepatics, in the number of new species proposed, in his narrow specific concept (cf. Verdoorn, 1934, p. 2), and, above all, in his preparation of a comprehensive treatment of all the Hepaticae of the world, the *Species Hepaticarum* (1898–1924).

Although the number of species of bryophytes known today may be estimated only with the greatest difficulty, because of the lack of any recent census, it is reasonably safe to suggest that, as of 1951, the world's known flora contains some 25,000 described species of Musci (Jaeger and Sauerbeck, 1870–1880; Paris, 1903–1906; Brotherus, 1901–1909, 1924–1925), nearly 350 species of *Sphagnum* (Warnstorf, 1911; Paul, 1924) and perhaps 10,000 species of hepatics (Schiffner, 1893–1895; Stephani, 1898–1924). Of course, the warning must be interjected hastily that the numbers just quoted refer to species *described*, but with no guarantee that they actually exist in nature, since, just as in other groups of organisms, too many species have been proposed as new several times, under different names, or else created in the first place on insufficient grounds (cf. Fleischer, 1922; Andrews, 1951; Verdoorn, 1934, p. 2), indicating that at least some of the figures cited may eventually have to be scaled downward.

It seems appropriate to devote some space to a brief account of the progress made in floristic studies of the world's bryophytes, especially since no survey of this sort has appeared for twenty years. Europeans initiated the study of bryophytes, and Europe continues to be the center for research in bryology, in spite of increasing activity in this field in other parts of the world, especially in the United States. Consequently, the bryophytes of Europe are by far the best known, and the publications concerning them seem to be almost innumerable. In 1853, one of the most important bryological floras ever published, which still sets a high standard both for illustration and for descriptions, neared completion. This work, the *Bryologia Europaea* (Bruch, Schimper and Gümbel, 1836–1855) appeared at irregular intervals in fascicles of varying numbers of pages over a period of nearly twenty years (Barnhart, 1944). Since the completion of the *Bryologia Europaea* many further important publications covering the bryophytes of Europe have appeared, of which especial mention should be made of the valuable contributions of Limpricht (1885–1903) and of Mönkemeyer (1927) on the mosses, and of K. Müller (1905–1916, 1951) on the hepatics, in Rabenhorst's *Kryptogamen-Flora von Deutschland, Österreich und der Schweiz.* The works of Roth (1904–1905) and Schiffner (1901–1937) also deserve mention.

The bryophyte flora of almost every individual European country has been treated fully, and sometimes repeatedly, by substantial publications. Examples of outstanding contributions for different countries are: for Great Britain, those by Braithwaite (1880–1905), Pearson (1902), Dixon (1924), Macvicar (1926), and Sherrin (1927); for Spain and Portugal, by Casares-Gil (1919–1932), Freitas (1948), Allorge (1947), and Cortés Latorre (1951); for Italy, by De Notaris (1869), Zodda (1934), and Giacomini (1947); for France, by Husnot (1884–1890, 1922); for Belgium, by Demaret (1945), and Vanden Berghen and Duvigneau (1943); for Germany, by many authors, including several excellent provincial floras (cf. Mönkemeyer, 1927); for the east Baltic area, by Malta (1931); for Denmark, by Jensen (1915, 1923); for Sweden, by Möller (1911–1936); for Norway, by Jørgensen (1934); for Scandinavia as a whole, by Brotherus (1923), Arnell (1928), and Jensen (1939); for Austria, by Juratzka (1882), and Gams (1950); for Switzerland, by Amann (1912), and Meylan (1924); for Czechoslovakia by Pilous (1948); for Slovakia by Smarda (1948); for Dalmatia by Latzel (1931), and K. Müller (1948b); and for Russia by Warnstorf (1912–1913), Saviez (1936b), Saviez and Ladyzhenskaja (1936), and Lazarenko (1951).

The study of bryology in North America remained much neglected during the first half of the last century, in spite of the great activity shown in Europe. The excellent early works that did appear are consequently all the more important, and among them should be cited those of Sullivant (1856, 1864, 1874), Lesquereux and James (1884), and Macoun and Kindberg (1892, 1902). During the past fifty years, however, the study of bryophytes developed rapidly in North America, and many important floristic studies have been published, culminating in the monumental works of Grout (1928–1940) on Musci and of Frye and Clark (1937–1947) on Hepaticae, which cover all of North America north of Mexico. Other bryological works of more restricted geographical application cover the eastern United States (Grout, 1903–1908; Dunham, 1951), the northwestern United States (Clark and Frye, 1928; Jones, 1930), Alaska (Cardot and Thériot, 1902; Persson, 1952), California (Howe, 1899), Connecticut (Evans and

Nichols, 1908), Florida (Kurz and Little, 1933), Michigan (Steere, 1950), New York (Grout, 1916; Schuster, 1949), Oregon (Sanborne, 1929), Ohio (Henderson, 1927–1931), Pennsylvania (Jennings, 1951), Tennessee and North Carolina (Sharp, 1939), Vermont (Grout, 1898), and West Virginia (Ammons, 1940).

An intensive search for new trade routes by various European governments during the last century led to a series of explorations within the arctic regions, which continued under various auspices and resulted in important bryological discoveries. Among the important works on the bryology of arctic Europe and Asia may be listed those of Arnell (1892), Arnell and Jensen (1907–1910), and Brotherus (1923) for northernmost Scandinavia; of Lid (1924), Savicz and Arnell (1947) for Novaya Zemlya; of Hesselbo (1918) and Meylan (1940) for Iceland; of Lid (1941) and Hesselbo (1924) for Jan Mayen Island; of Arnell (1900), Berggren (1875), and Persson (1942) for Spitzbergen; of Savicz (1936a), and Størmer (1940) for Franz Josef Land; of Arnell (1913, 1917), Lindberg and Arnell (1889–1890), and Savicz (1924) for the mainland of arctic Asia, and of Savicz (1936a) for Severnaïa Zemlya.

Unfortunately, the bryological flora of Greenland lacks any unified treatment later than the useful catalogue published by Lange and Jensen (1887), although the more recent volumes of *Meddelelser om Grønland* contain many important contributions to our knowledge of the bryophytes of Greenland. The bryophytes of arctic America have received considerable attention, as evidenced by the publications of Bryhn (1906–1907), Hesselbo (1937), Williams (1921), Polunin (1948), and Steere (1948b, 1951).

The continent of Asia still possesses many areas that are unknown bryologically, and no recent synoptical study of all Asiatic bryophytes exists. Many important reports covering different regions have been published, however, of which outstanding examples are those of Brotherus (1892), and Woronoff (1930) on the Caucasus; of Mitten (1859), Brotherus (1928), Kashyap (1929, 1932), Chopra (1943), and Brühl (1931) on India; of Dixon (1937) on Assam; of Reimers (1931) and Bartram (1935) on China; of Brotherus (1929) and of Nicholson, Herzog and Verdoorn (1930), on southwest China; of Kabiersch (1936, 1937), and of Chen (1941) on eastern Asia; of Iishiba (1929–1932, 1931), Horikawa (1934–1951), and Hattori (1951) on Japan; of Cardot (1905) on Formosa; of Bartram (1943) on Burma; of Dixon (1935) on Siam; and of Bartram (1939) on the Philippine Islands.

The bryophyte flora of Malaysia has received much investigation, and substantial contributions have been made by Schiffner (1898) on the whole area; by Schiffner (1900) and Fleischer (1904–1924) on Java; by Bartram (1942, 1945) on New Guinea; by Dixon (1932) on Sumatra and (1934) on the Celebes; and by Herzog (1950) on Borneo.

The bryological flora of Africa, like that of Asia, remains known only in part, although numerous excellent studies on different regions, especially the more temperate ones, have been published. From northern Africa and its islands we can cite the works of Trabut (1942), Gattefosse and Werner (1932), Luisier (1927, 1945), and the Allorges (1948). For southern Africa should certainly be mentioned the outstanding works of Renauld and Cardot (1915) on Madagascar and of Sim (1926) on South Africa. The bryology of Madagascar recently received review by Jovet-Ast (1948a, 1948b). Only a very few major works concerned with the more tropical areas of Africa have appeared, examples of which are those of Potier de la Varde (1928, 1936) on Oubangui and Gabon; of Demaret (1940) for the Belgian Congo; of Cufodontis (1951) for Ethiopia; of Paris (1908) on French Guinea; and of Dixon (1938) on tropical East Africa.

The bryophytes of tropical North America have been the subject of numerous investigations. Mexico, especially, has received much attention from bryologists, as indicated by the excellent publications of Bescherelle (1872), Gottsche (1867), Thériot (1933), and Crum (1951a, 1951b).

The Central American republics range from well known to almost unknown, bryologically speaking, as shown by examples of relatively recent publications on Guatemala (Bartram, 1949); British Honduras (Steere, 1946a); El Salvador (Steere and Chapman, 1946); Honduras (Crum, 1952b); Costa Rica (Bartram, 1951; Herzog, 1951); Nicaragua (Crum, 1952a), and Panama (Crum and Steere, 1950).

Bryological studies of the West Indies have resulted in many significant works, of which examples are those of Thériot (1939–1941) on Cuba and (1944) on Hispaniola; of Pagán (1939) on Puerto Rico and (1942) on Guadeloupe; of Bescherelle (1876) and Brotherus (1903) on the French Antilles; of Britton (1921) and Evans (1911) on the Bahamas; and of Bartram (1936a) on Jamaica.

The enormous collections made by the hepaticologist Richard Spruce (cf. Wallace, 1908) between 1849 and 1864, during his explorations of the Amazonian basin of the Andes of Ecuador and Peru and of the headwaters of the Orinoco River in the hinterland of Colombia and Venezuela, immeasurably furthered the progress of our knowledge of the bryology of South America. Spruce's great collections formed the basis for two important works, the very useful treatment of all tropical American mosses by Mitten (1869), and the magnificently original report on his hepatics by Spruce himself (1885). In spite of the voluminous literature on the bryophytes of South America, very few general works have been published since those of Spruce and Mitten. Besides the exceptionally fine publications of Herzog (1916, 1920), based on his own collections in Bolivia, useful reviews of the bryophytes of different South American republics have been produced by Pittier (1936) for Venezuela, by Kühnemann (1938) for Argentina, by Brotherus (1920) for Peru and (1924b) for Brazil, by Thériot (cf. Potier de la Varde, 1948) for Chile, by Herter (1933) for Uruguay, by Richards (1934) for British Guiana, and by Steere (1948c) for Ecuador.

In spite of its remoteness the southernmost region of South America has received a surprisingly large amount of attention from collectors of bryophytes because of the numerous visits there of expeditions studying the south polar regions. The important general report by Cardot (1908) should be cited here, as well as more recent works by Stephani (1911), Cardot and Brotherus (1923), and Roivainen and Bartram (1937). Several bryophytes have been reported from the Antarctic Continent itself, in spite of its extraordinarily inhospitable climate (Cardot, 1913; Bartram, 1938b).

The bryophytes of New Zealand are now reasonably well known through the synoptical work of Dixon (1913–1929) and the contributions of Hodgson (1950). Australia, on the other hand, in spite of its much greater area, has received less study. Since the census of mosses published by Watts and Whitelegge (1902–1905), no further general work has appeared, although important original contributions have been made on different regions by Brotherus (cf. Fleischer, 1929), Dixon (cf. Bartram, 1944), and others.

Many of the islands of the various great oceans have been the subject of bryological studies, of which illustrative examples are on the Seychelles (Dixon, 1929), Hawaii (Bartram, 1933b), Fiji (Bartram, 1936b, 1948, 1950), southeastern Polynesia (Bartram, 1940), Raiatea (Bartram, 1931b), Solomon Islands (Bartram, 1938a), Tristan de Cunha (Dixon, 1939), Gilbert Islands (Dixon, 1927), Galápagos Islands (Bartram, 1933a), Juan Fernández and Easter Island (Brotherus, 1924a; Evans, 1930; Herzog, 1942).

The limited space available for this review prevents the inclusion of numerous important papers on the bryology of many parts of the world. However, this fault may be remedied in large part by reference to the biographies and bibliographies of the great investigators of exotic bryophyte floras, as Bescherelle (cf. Camus, 1903), Britton (cf. Barnhart, 1935), Brotherus (cf. Fleischer, 1929), Cardot (cf. Thériot, 1935), Dixon (cf. Bartram, 1944), Evans (cf. Nichols, 1938), Fleischer (cf. Verdoorn, 1931), Gottsche (cf. Husnot, 1893), Grout (cf. Steere, 1948a), Loeske (cf. Jäggli, 1935), Mitten (cf. Nicholson, 1907), Paris (cf. Husnot, 1911), Renauld (cf. Thériot, 1910), Spruce (cf. Stephani, 1894), Stephani (cf. Beauverd, 1928), Sullivant (cf. Rodgers, 1940), and Williams (cf. Steere, 1945).

Monographic Studies

In spite of the great advances made in floristic and geographic studies during the last century, the preparation of critical monographic studies of different genera and families of bryophytes has been greatly neglected, as pointed out by Verdoorn (1934, 1950) and by Malta (1936). With too few specialists and too little support of a field without direct economic implications as well as lack of support for publication, purely systematic studies have suffered. Outstanding monographic works, even on a regional basis, are conspicuous by their relative rarity, and whole groups of bryophytes remain in utter confusion because of the large numbers of species described with little or no reference to those already in existence. The classic older series of monographs on the mosses of Europe, the *Bryologia Europaea* (Bruch, Schimper and Gümbel, 1836–1855), has been reinforced by detailed treatments of the Funariaceae and Grimmiaceae by Loeske (1929, 1930). Excellent monographic revisions of several families of bryophytes of North America, covering the whole continent, have appeared in Volumes 14, 15 and 15A of *North American Flora,* supported and published by the New York Botanical Garden. Contributions on the Marchantiales by Howe and Evans, on *Sphagnum* by Andrews, and on various families of mosses by Britton, Williams and others—and more recently on the Orthotrichaceae and Fissidentaceae by Grout—furnish indispensable aids to a knowledge of the bryophytes of North America. Some examples of the other fundamental monographic studies of the century (with special emphasis on the more recent ones) concern Acromastigum (Evans, 1934), Bazzania (Fulford, 1946); Ceratolejeunea (Fulford, 1945), Drepanolejeunea (Herzog, 1939), Frullaniaceae and Lejeuneaceae Holostipae (Verdoorn, 1930, 1934), Micropterygium (Reimers, 1933), Plagiochila (Dugas, 1928; Carl, 1931; Herzog, 1932, 1938), Pycnolejeunea (Hoffman, 1935), Radula (Castle, 1950), Scapania (K. Müller, 1905; Buch, 1928), Taxilejeunea (Eifrig, 1937), Sphagnum (Warnstorf, 1911; Andrews, 1913), Anacolia (Flowers, 1952), Bryum (Podpěra, 1942–1951), Calliergon (Wynne, 1945), Cyclodictyon (Demaret and Potier de la Varde, 1951), Daltonia (Bartram, 1931a), Dawsonia (Burges, 1949), Drepanocladus (Wynne, 1944a, 1944b; Tuomikoski, 1949), the Fontinalaceae (Cardot, 1892), Haplocladium (Thériot, 1930; Reimers, 1937), Orthodontium (Meijer, 1951), Orthotrichum (Piccioli, 1932), Pilosium and Stereophyllum (Grout, 1945), Plagiothecium (Jedlička, 1948), Pottia (Warnstorf, 1916), Ulota (Malta, 1933), and Zygodon (Malta, 1926).

Bryogeography

Just as the line between monographic and floristic studies is not always easy to define, so we also find complete intergrading between floristic and bryogeographic investigations. Naturally, a knowledge of the species concerned forms a major basis for the derivation of any general principles of geographic distribution. Herzog (1926; in Verdoorn, 1932) produced for the first time a clear-cut survey of the general features of the distribution of bryophytes throughout the world. Irmscher (1929) contributed some original ideas concerning the significance of present distributions of mosses on the different continents, in the light of the Wegenerian theory of continental drift. Domin (1923) made a major contribution to our knowledge of the world distribution patterns of Hepaticae. Du Rietz (1940) used bryological materials rather extensively in his study of the problems of bipolar plant distribution. One of the most detailed and helpful works on bryogeography yet to appear is that of Amann (1928), ostensibly covering Switzerland, but really of wide application to most of Europe and much of the rest of the world, with especial reference to the effect of habitat and climate on distribution. Although truly enormous, the literature on local and regional studies of bryophytes and their distribution in Europe becomes reasonably accessible through several modern publications (cf. Mönkemeyer, 1927; Möller, 1911–1936; Blaringham, 1944; Allorge, 1947; K. Müller, 1951; and in the pages of *Revue Bryologique*). Precise studies on the distribution of bryophytes in North America, and of the various factors affecting their distribution, are distressingly few. Attention has been called to special problems of disjunct distribution by Steere (1938), Schornherst (1943), and Sharp (1944), and the erratic distribution of a few species has been related to the maximum extent of Pleistocene glaciation (Steere, 1937; Wynne, 1944a, p. 647). Fulford (1951) has provided a stimulating analysis of the distribution patterns of Hepaticae in South America. In spite of long interest in the geographical distribution of bryophytes and an extensive literature on regional bryophyte floras we have identified only the most generalized types of geographic elements over much of the world, and the known distribution of most species of tropical bryophytes reflects, upon careful analysis, only the distribution of botanical collectors.

Ecology

Our knowledge of the ecology of bryophytes progressed greatly during the past century, although even the earliest bryologists were impressed by the clear-cut correlations between bryophytes and their habitats, and especially by the remarkable restriction of some species to very specific substrata. Excellent reviews of progress in our understanding of the associations of bryophytes have been given by Gams (in Verdoorn, 1932) and by Gimingham and Robertson (1950). It is encouraging to note the greatly increasing use of bryological data in general studies of plant sociology, primarily in Europe, as for example in those of Braun-Blanquet (1948) and Du Rietz (1949). A brief comparison of the pages of the *Journal of Ecology* (British) and of *Ecology* (American) will demonstrate rather conclusively the extensive utilization of bryological data by European ecologists and the serious neglect of such data by American workers, with a few outstanding exceptions. The autoecological aspects of bryology have been studied even more than the sociological ones, although the two approaches are often not too well distinguished by workers. Richards (in Verdoorn, 1932) has provided an excellent review of the effect of environmental factors on the distribution of bryophytes, and has also compiled a useful list of ecological literature (1940). Examples of some recent ecological papers with emphasis on bryological communities and successions follows: on the bryophytes of bogs and swamps (Sjörs, 1948), of aquatic habitats (Sörensen, 1948), of the trunks of living trees (Phillips, 1951), of bare soils (Waldheim, 1947), of the steppes of Hungary (Gams, 1934), on sand (Jalas, 1950), on granite rock (Keever, Oosting and Anderson, 1951), on volcanic ash (Griggs, 1935), on the leaves of higher plants (Schiffner, 1929; Vanden Berghen, 1949), on rotting wood and on shaded rocks (Jovet and Jovet, 1944), and of snow-beds (Gjaervoll, 1950). Examples of recent ecological studies emphasizing the effects of different environmental factors with relation to the distribution of bryophytes concern the effect of bark composition (Billings and Drew, 1938), of hydrogen-ion concentration (Meyer and Ford, 1943; Apinis and Diogues, 1933; Apinis and Lacis, 1936; Sörensen, 1948), of nitrogen lack (Griggs, 1934), of water depth (Persson, 1944a), of low temperatures (Koppe, 1931; Becquerel, 1949; Morrill, 1950), of evaporation (Potzger, 1939), of brackish water (Luther, 1951), of burning (Doignon, 1949), of mineral soils (Persson, 1948), of drying out (Hofleur, 1942; Buch, 1947a), of trace elements (Biebl, 1947), of wave length of light (Teodoresco, 1929), and of wind (Persson, 1944b).

Morphology

The distinctive morphology of bryophytes early attracted much attention which resulted in several discoveries important in developing general botanical principles. Although the life history of bryophytes was known in a superficial way from the beginning of the nineteenth century, the regular alternation of sexual and asexual generations was not clearly demonstrated until the exact beginning of the very century under consideration (Hofmeister, 1851). The concomitant cytological significance of an alternation of a diploid, spore-producing generation with a haploid, gamete-producing generation was not recognized until considerably later, however; apparently by Strasburger (1894). These two great discoveries set into motion a long series of serious and detailed investigations, by means of which we now know much about the behavior and structure of many groups of bryophytes. The impressive works of Leitgeb (1874–1881), Bower (1935), Campbell (1940), and Goebel (1930–1933) not only summarize the status of bryological morphology of the time, but also include much new material resulting from original research. Smith's modern reference book (1938) brings together in an exemplary fashion most of the literature of this field.

Experimental Morphology

The discovery of anomalous behavior in the life cycle of bryophytes gave an opening for experimental investigations which, in turn, led to a greater understanding of alternation of generations, or at least of the problems involved. Pringsheim (1878) noted that under certain circumstances the seta of a moss sporophyte would produce, through local regeneration, a filamentous protonema, ordinarily considered to be a gametophytic structure. Furthermore, the protonema so originated continues its development in a perfectly normal manner and eventually produces the characteristic green leafy gametophyte plants. Considerably later, the cytological significance of apospory was realized, and stimulated further researches such as those of the Marchals (1911), who were able to produce polyploidy under controlled conditions for the first time. The cytological and genetical implications of these brilliant experiments were obvious, and led to the extensive researches of Wettstein (1942; in Verdoorn, 1932), whose work on the genetics of mosses, in connection with regeneration, apospory, and hybridization between species and genera, is now classic. Some study of apospory in Hepaticae has also been made (Rink, 1935). Springer (1935) reported the bypassing of fertilization, or apogamy, through the direct budding off of a sporophytic structure from gametophytic tissue in a moss, as the result of experiments that have not yet been repeated. Investigation of the ability of bryophytes to reproduce asexually through various vegetative means, as gemmae, brood-bodies, etc., has led to an extensive literature (Degenkolbe, 1937; Correns, 1899; Sainsbury, 1952). Because of their sensitive responses to small variations in environment bryophytes furnish good materials for experimental research, but are not yet sufficiently appreciated, in spite of some excellent work on them (Buch, in Verdoorn, 1932). Research on bryophytes utilizing the techniques of experimental morphology have yielded results of importance to plant physiology (Buch, 1947b; La Rue, 1942; Biebl, 1947), to genetics (Wettstein, 1942), to ecology (Dombrowski, 1933; Romose, 1940), and to systematic bryology (Wettstein and Straub, 1942; Arnaudow, 1938). Ernst-Schwarzenbach (1944) demonstrated experimentally the relationship between spore dimorphism and sexuality in mosses.

Anatomy

Although the more detailed structural aspects of descriptive morphology are placed under the heading of anatomy by many authors, the two fields are exceedingly difficult to distinguish. Nevertheless, unusually complete treatises and summaries have been published on the anatomy of Hepaticae by Herzog (1925), Buch (in Verdoorn, 1932), and K. Müller (1951), and of Musci by Lorch (1931) and van der Wijk (in Verdoorn, 1932).

Physiology

Bryological materials have been used relatively rarely in physiological experiments, and the only comprehensive review concerned with the physiology of bryophytes seems to be that of Garjeanne (in Verdoorn, 1932). In spite of its simplicity of structure and behavior, in comparison with higher forms, the bryophyte plant resembles the vascular plant very closely in its physiological processes. Since the publication of Garjeanne's excellent review, important physiological studies have been made on bryophytes, of which examples are those of Bowen (1933), Mägdefrau and Wutz (1951), Roberts and Haring (1938), and Buch (1947b) on water relations; of Biebl (1947) on the effect of trace elements; of Meyer and Ford (1943) on the effect of hydrogen-ion concentration; of Voth (1943) and Fulford, Carroll and Cobbe (1947) on the responses to variations in the nutrient solutions; of Fulford and Kersten (1947) on reaction to X rays; of Ståfelt (1937) on the gaseous exchange of bryophytes; of Walsh (1947) on geotropism and phototropism in the sporophyte of *Splachnum;* of Hagerup (1935) and Meusel (1935) on growth; of Patterson (1946) on osmotic pressure; and of Meyer (1941) on spore longevity. Many of the researches on the autoecology of bryophytes are essentially physiological in their approach and in their results, as for example the work of Dombrowski (1933) on spore distribution, the very detailed study of *Homalothecium sericeum* with relation to its environment by Romose (1940), and the researches on drought resistance by Patterson (1943).

Cytology

Since the tissues of bryophytes are relatively uncomplicated, consisting in many structures of a single layer of cells, they furnish favorable material for cytological observations. The behavior of the cytoplasm and of the cell as a whole in bryophytes has received considerable attention, and the researches on these broader aspects of the cytology of bryophytes has been the subject of an excellent review by Motte (in Verdoorn, 1932). Some observations were made on the behavior of chromosomes in bryophytes well over fifty years ago, and Allen discovered the first sex chromosomes known in plants in the hepatic, *Sphaerocarpus,* more than thirty-five years ago. However, the most comprehensive work on the cytology of bryophytes dates from the past twenty-five years, with steadily gained momentum through the years, so that a large body of valuable information has accumulated. Several excellent reviews of cytological investigations of bryophytes have appeared, by Höfer (in Verdoorn, 1932), by Döpp (1937), by Sinoir (1952), and, for hepatics only, by K. Müller (1951). Cytotaxonomic investigations of bryological problems have begun only very recently, and already indicate that this approach will prove as helpful in understanding the relationships of bryophytes as it has in *Crepis,* for example. Haupt (1933), Heitz (1942), Lowry (1948), and Vaarama (1950) pioneered the field of cytotaxonomy of bryophytes. Jachimsky (1935) investigated the relationship between sex chromosomes and heterochromatin, with results of wide application elsewhere. So far, bryophytes have received relatively little attention as material for experimental cytology, in spite of such obvious advantages as their transparent tissues and ease of culture. Wolcott (1941) and Heitz (1945) have investigated the effects of colchicine on nuclear behavior in hepatics and mosses.

Genetics

Technical difficulties of various kinds and the inherent complexity of two alternating generations in bryophytes have tended to restrict genetical research in this group, so that their genetical behavior is still rather incompletely understood. Nevertheless, several very important programs of research on the genetics of bryophytes have been carried on through the last half-century. The discovery of sex chromosomes in *Sphaerocarpus* by Allen led him to a series of investigations (Allen, 1945) on the genetics of this genus, lasting more than twenty years. The extensive researches of Wettstein on the genetics and experimental morphology of mosses are classics (1942; in Verdoorn, 1932). His data do not indicate clearly that inheritance in mosses follows any simple Mendelian system, and therefore give real incentive for continued work, especially in view of the remarkable techniques that he invented. Burgeff (1943) gives us the results of an extraordinarily detailed monographic investigation of the genetics and genetic mechanisms of *Marchantia.* Further genetical study of different groups of bryophytes is still very much to be desired (cf. Sinoir, 1952). It would seem that the different behavior of the same chromosomes in haploid and diploid conditions, producing respectively a gametophyte and a sporophyte plant of very different appearance, would make an excellent problem for investigation.

Classification

At the end of a century during which matters of classification received much thoughtful consideration, we find that the generally accepted subdivisions of the division (or phylum) Bryophyta are three classes, the Hepaticae, the Musci, and the Anthocerotae, although the last-named group is considered by many botanists to be only an order within the class Hepaticae (Fritsch, 1929). Considerable evidence supports the separation of the present order Sphagnales from the Musci, and further study may very well see the acceptance of this group as a separate class (Chalaud, 1945). Detailed studies in any group of plants tends to bring out fundamental differences hitherto unnoticed and to result in an increase in the number of classes or even of divisions, as has occurred in Algae (Smith, 1938). The philosophical aspects of systematic bryology have been considered by several authors, and considerable progress made in correlations between the morphology of bryophytes, their classification, and the nature of species and other taxonomic groups. One of the most distressing aspects of bryophytes to the person who may wish to classify them in an orderly manner is the fact that the gametophyte and sporophyte generations have evolved with no relation to each other, in very different directions, so that in some groups we find a conservative gametophyte and a very variable, rapidly evolving sporophyte, whereas in other groups we find just the opposite situation. Although a relatively small group compared with the Musci, the Hepaticae have received a disproportionate amount of attention, as compared with mosses, from the aspects of phylogeny, evolutionary sequences, and special morphology, perhaps because of the diverse nature of the group and the many families and genera with a single or very few representatives. The results of these studies appear in the standard references on plant morphology, but among the works of especial importance should be cited those of Schiffner (1917) and Fulford (1948). K. Müller (1948a) offers a thoughtful discussion of the species problem and specific criteria in Hepaticae. The numerous problems involved in the classification of Hepaticae have attracted a great deal of attention, and reasonably stable arrangements have been established (Verdoorn, 1932; Evans, 1939). In mosses, some very fundamental ideas have been brought forth by Loeske (1910, 1935) with regard to the systematics, phylogeny, and species problem of this group. The most widely accepted classification of Musci at present is that proposed by Fleischer (1920, 1904–1924), and established on a still firmer basis by Brotherus (1924–1925). Dixon (in Verdoorn, 1932) gives one of the most recent views on the classification of Musci. The concept of genera in Musci and its attendant problems has been discussed by Steere (1947).

Phylogeny

The phylogeny of bryophytes has been investigated by several methods, most commonly through studies of the comparative morphology of living forms (Loeske, 1910; Schiffner, 1917), through the use of serological tests (Stepputat and Ziegenspeck, 1929), and through the study of fossil forms (Harris, 1939; Barkman, 1950). Although earlier morphologists proposed that the Bryophyta are derived directly from the Chlorophyceae, from the Phaeophyceae (Church, 1919), or from some common ancestor of the Pteridophyta, the recent discovery of primitive Devonian psilophytes, *Rhynia* and *Hornea,* with more than a superficial resemblance to members of the Anthocerotae, suggests that the Bryophyta may be reduction forms of some group of primitive pteridophytes (Smith, 1938; Haskell, 1949). Zimmerman's excellent review (in Verdoorn, 1932) summarizes in concise fashion the ideas on bryological phylogeny.

Paleobryology

The large number of bryophytes that have been discovered in fossil condition is surprising, in view of the lack of lignified or of heavily cutinized tissues in these plants. Thallose hepatics of a distinctly modern appearance are well known from Carboniferous deposits in England, and there is some evidence for the existence of mosses during the same epoch (Walton, 1928). Harris (1938, 1939) provides excellent accounts of Naiadita, a fossil bryophyte from the Triassic of England, in so complete and detailed a fashion that a good deal of light is shed on the ancestral forms of present-day bryophytes. Dixon (1927) listed very completely the fossil Musci reported up to that time, and a survey of the Cenozoic and Mesozoic bryophytes of North America has appeared rather recently (Steere, 1946b). Most of the bryophytes known in fossil condition are relatively recent, occurring in Pleistocene and post-Pleistocene deposits, so that a great many of them might be termed subfossil. As might be expected, a large proportion of the Quaternary bryophytes still survive at the present time. Because of their excellent state of preservation, these subfossil specimens are easily identified through the use of modern manuals, and consequently are of real value in investigations of geographic distribution of the plants of former times (Gams, in Verdoorn, 1932), as indicators of interglacial climates (Steere, 1942), and to supplement data gained through pollen studies (Meijer, 1950). This modern and useful aspect of bryology has yet been hardly touched.

Summary

The past century has produced substantial progress in the field of bryology, especially in descriptive systematics, floristics, and morphology. The application of experimental methods to bryophytes began so late, relatively, that investigations on the physiology, cytology, genetics, and experimental morphology of these plants have been pioneer enterprises. A more general interest in bryophytes and a realization of their many advantages as experimental material will lead to a much greater utilization of them. In this connection, it should be pointed out that there is a significant increase in the number of nontechnical (but not unscientific) handbooks and publications of broad interest, designed for the general botanist and for amateurs. Some of the most recent examples are *Woodland Mosses* by Watson (1947), *Moser fra Skog og Myr* by Størmer (1946), *A Book of Mosses* by Richards (1950), *How to Know the Mosses* by Conard (1944), *Mosses With a Hand-Lens* by Grout (1947), and two Swedish publications lavishly and beautifully illustrated in color (Ursing, 1949; Nannfeldt and Du Rietz, 1945). Although European botanists in general are very well aware of the importance of bryophytes as a source of supplementary data in phytogeographical and ecological studies and as providing excellent material for experimental researches, American botanists still tend to underestimate their value. Consequently, the trend toward the popularization of bryology through nontechnical works is highly desirable, especially in this country.

BIBLIOGRAPHY

ALLEN, CHARLES E.

1945. The genetics of bryophytes. II. Bot. Rev., 11:260–287.

ALLORGE, PIERRE

1947. Essai de bryogéographie de la Péninsule Ibérique (doc. réunis par Mme. Pierre Allorge). 114 pp., 8 pls., 2 maps. Paris: P. Lechevalier.

ALLORGE, VALIA, and PIERRE ALLORGE

1948. Végétation bryologique de l'île de Flores (Açores). Rev. Bryol. et Lichénol., n.s., 17:126–164.

AMANN, JULES

1928. Bryogéographie de la Suisse. x + 453 pp. Zurich: Fretz Frères.

AMANN, JULES, and CHARLES MEYLAN

1912. Flore des mousses de la Suisse. 215 + 414 pp. Lausanne: Imprimeries Réunies S.A.

AMMONS, NELLE

1940. A manual of the liverworts of West Virginia. American Midl. Nat., 23:3–164.

ANDREWS, A. LEROY

1913. Sphagnales—Sphagnaceae. N. Amer. Flora, 15(pt. 1):1–31.

1951. Studies in the Warnstorf Sphagnum herbarium. VI. The subgenus Inophloea in the eastern hemisphere. Bryologist, 54:83–91.

1951. Taxonomic Notes. X. The family Leptostomaceae. Bryologist, 54:217–223.

ANNALES BRYOLOGICI

1928–1939. A Yearbook Devoted to the Study of Mosses and Hepatics. Vols. 1–12 + suppl. vols. 1–4. Ed., Frans Verdoorn. Waltham, Mass.: Chronica Botanica Co.

APINIS, A., and A. M. DIOGUCS

1933. Data on the ecology of bryophytes. I. Acidity of the substrata of Hepaticae. Acta Hort. Bot. Univ. Latvien., 8:1–19.

Apinis, A., and L. Lacis

1936. Data on the ecology of bryophytes. II. Acidity of the substrata of Musci. Acta Hort. Bot. Univ. Latvien., 9/10(1934–1935):1–100.

Arnaudow, N.

1938. Künstliche Aenderungen des Moosperistoms. Ann. Bryol., 11:21–24.

Arnell, H. Wilh.

1892. Lebermoosstudien im nördlichen Norwegen. x + 44 pp. Jönköping: C. J. Lundgrens Enkas Boktryckeri.

1900. Beiträge zur Moosflora der Spitzbergischen Inselgruppe. öfversigt K. Svensk. Vet.-Akad. Förhandl., 57:99–130.

1913. Zur Moosflora des Lena-Tales, Bericht über die im Jahre 1898 von Herrn Doctor H. Nilsson-Ehle an der Lena gesammelten Moose. Arkiv Bot., 13(pt. 2):1–94.

1917. Die Moose der Vega-Expedition. Arkiv Bot., 15(pt. 5):1–111.

1928. Skandinaviens Flora. II. Mossor. a. Levermossor. 224 pp. Stockholm: P. A. Norstedt and Sons.

Arnell, H. Wilh., and C. Jensen

1907–1910. Die Moose des Sarekgebietes. Naturwiss. Untersuch. Sarekgebirges in Schwedisch-Lappland, 3:71–268.

Arnell, Sigfrid

1947. Contributions to the knowledge of the hepatics of Novaya Zemlya. Svensk. Bot. Tidskr., 41:209–217.

Barkman, Jan

1950. Over de phylogenie der Levermossen. Buxbaumia, 4:32–55.

Barnhart, John Hendley

1935. The published work of Elizabeth Gertrude Britton. Bull. Torrey Club, 62:1–17.

1944. Dates of the "Bryologia Europaea." Bryologist, 47:97–108.

Bartram, Edwin B.

1931a. A review of the American species of *Daltonia*. Bull. Torrey Club, 58:31–48.

1931b. Mosses of Raiatea. Occ. Pap., Bishop Mus., Honolulu, 9(pt. 16):1–14.

1933a. Mosses of the Templeton Crocker Expedition collected by John Thomas Howell and lists of the mosses known from the Galapagos Islands and from Cocos Island. Proc. Calif. Acad. Sci., ser. 4, 21:75–86.

1933b. Manual of Hawaiian mosses. Bishop Mus. Bull., Honolulu, 101:1–275. (Suppl.: Occ. Pap., 15(1939):93–108.)

1935. Additions to the moss flora of China. Ann. Bryol., 8:6–21.

1936a. New and noteworthy mosses from Jamaica. Journ. Washington Acad. Sci., 26:6–16.

1936b. Contribution to the mosses of Fiji. Occ. Pap., Bishop Mus., Honolulu. Vol. 11. *See also* Bartram, 1948, 1950.

1938a. Mosses of the Solomon Islands. Bryol., 41:127–132.

1938b. Second Byrd Antarctic Expedition—Botany. III. Mosses. Ann. Mo. Bot. Gard., 25:719–724.

1939. Mosses of the Philippines. Philip. Journ. Sci., 68:1–437.

1940. Mosses of southeastern Polynesia. Occ. Pap., Bishop Mus., Honolulu, 15:323–349.

1942. Third Archbold Expedition mosses from the Snow Mountains, Netherlands New Guinea. Lloydia, 5:245–292.

1943. Burma mosses. Farlowia, 1:171–189.

1944. Henry Neville Dixon. Bryologist, 47:137–144.

1945. Mosses of Morobe District, northeast New Guinea. Bryologist, 48:110–126.

Bartram, Edwin B. (Cont.)

1948. Additional Fijian mosses. I. Occ. Pap., Bishop Mus., Honolulu. Vol. 19.

1949. Mosses of Guatemala. Fieldiana: Bot., 25:1–442.

1950. Additional Fijian mosses. II. Occ. Pap., Bishop Mus., Honolulu. Vol. 20.

1951. Additional Costa Rican mosses. IV. Bryologist, 54:231–242.

Beauverd, Gustave

1928. Franz Stephani (15 avril 1842—23 février 1927). Bull. Soc. Bot. Genève., sér. 2, 19:334–343.

Becquerel, P.

1949. L'action du froid sur la cellule végétale. Botaniste, 34:57–73.

Berggren, Sven

1875. Musci et Hepaticae Spetsbergenses. Bericht über die Untersuchung der Moosflora Spitzbergens und Beeren-Eilands während der Schwedischen Expeditionen 1864 und 1868, und Verzeichniss der dort gesammelten Arten. K. Svensk. Vet.-Akad. Handl., 13(pt. 7):1–103.

Bescherelle, Émile

1872. Prodromus bryologiae Mexicanae ou énumération des Mousses du Mexique avec description des espèces nouvelles. Mém. Soc. Natl. Sci. Nat. Cherbourg, 16:145–256.

1876. Florule bryologique des Antilles françaises. Ann. Sci. Nat. Bot., sér. 6, 3:175–265.

Biebl, R.

1947. Ueber die Gegensätzliche Wirkung der Spuren Elemente Zink und Bor auf die Blattzellen von *Mnium rostratum*. Oesterr. Bot. Zeitschr., 94:61–73.

Billings, W. Dwight, and William B. Drew

1938. Bark factors affecting the distribution of corticolous bryophytic communities. Amer. Midl. Nat., 20:302–330.

Blaringhem, Louis

1944. Pierre Allorge (1891–1944) et la géographie botanique raisonnée. Ann. Sci. Nat. Bot., sér. 11, 5:1–22.

Bowen, Esther J.

1933. The mechanism of water conduction in the Musci considered in relation to habit. Ann. Bot., 47:401–422, 635–661, 889–912.

Bower, F. O.

1935. Primitive Land Plants also Known as the Archegoniatae. xiv + 658 pp., 465 illus. London: Macmillan and Co.

Braithwaite, Robert

1880–1905. The British Moss-Flora. 3 vols. London: L. Reeve and Co.

Braun-Blanquet, J.

1948. La végétation alpine des Pyrénées orientales. Comm. Sta. Internat. Géobot. Méditerr. et Alp., 98:1–306.

Britton, Elizabeth G.

1921. Bahama mosses. Bryologist, 24:17–19.

Brotherus, Viktor F.

1892. Enumeratio muscorum Caucasi. Acta Soc. Sci. Fennicae, 19(pt. 12):I–IV, 1–170.

1901–1909. Musci (Laubmoose). III. Unterklasse Bryales: II. Spezieller Teil. *In* Engler and Prantl, Die natürlichen Pflanzenfamilien. Teil I, Abt. 3, pp. 277–1246.

Brotherus, Viktor F. (Cont.)

1903. Musci Novi Dussiani. *In* Urban, Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis, 3:421–429.

1920. Musci Weberbaueriani. Beibl. Bot. Jahrb. 56 (Heft 2, no. 123):1–130.

1923. Die Laubmoose Fennoskandias. Flora Fennica I. xiii + 635 pp. Helsingfors: Akadem. Buchhandlung.

1924a. The Musci of the Juan Fernandez Islands. *In* Skottsberg, Natural History of Juan Fernandez and Easter Island, 2:409–448.

1924b. Musci (Laubmoose). Ergebnisse der Botanischen Expedition der Kaiserlichen Akademie der Wissenschaften nach Südbrasilien 1901, 2:251–358.

1924–1925. Musci (Laubmoose). *In* Engler and Prantl, Die natürlichen Pflanzenfamilien. 2nd ed., Vols. 10, 11. Leipzig: W. Engelmann.

1928. Contributions à la flore bryologique du Cachemire. Ann. Bryol., 1:28–46.

1929. Musci. *In* H. Handel-Mazzetti, Symbolae Sinicae, 4:1–147. Wien: J. Springer.

Bruch, Ph., W. Ph. Schimper, and Th. Gümbel

1836–1855. Bryologia Europaea. 65 fasc. in 6 vols., 636 pls. Stuttgart: E. Schweizerbart.

Brühl, P.

1931. A census of Indian mosses with analytical keys to the genera . . . Rec. Bot. Surv. India, 13 (pt. 1):1–135; (pt. 2):1–152.

Bryhn, Nils

1906–1907. Bryophyta in itinere polari norvagorum secundo collecta (Fortegnelse over de under den 2den Norske Polarexpedition indsamlede Moser). Report, 2nd Norwegian Arctic Expedition in the "Fram," 1898–1902, 11:1–260.

Bryologische Zeitschrift

1916–1917. Ed., Leopold Loeske. 1 vol. Berlin-Schöneberg: Hoffmann u. Campes Verlag (Max Lande).

Bryologist, The

1898– Journ. Amer. Bryol. Soc. Vol. 57 in 1954. Ed., William C. Steere, Stanford Univ., Calif.

Buch, Hans

1928. Die Scapanien Nordeuropas und Sibiriens. II. Systematischer Teil. Soc. Sci. Fennica, Comment. Biol., 3 (pt. 1):1–173.

1947a. De l'adaptation des Bryophytes, des Algues et des Lichens aux conditions d'humidité et de la concentration de la solution nutritive dans les milieux naturels. Rev. Bryol. et Lichénol., n.s., 16:54–59.

1947b. Über die Wasser- und Mineralstoffversorgung der Moose. II. Soc. Sci. Fennica, Comment. Biol., 9 (pt. 20):1–61.

Burgeff, H.

1943. Genetische Studien an Marchantia. Einführung einer neuen Pflanzenfamilie in die genetische Wissenschaft. viii + 296 pp. Jena: G. Fischer.

Burges, Alan

1949. The genus *Dawsonia*. Proc. Linn. Soc. New South Wales, 74:83–96.

Buxbaumia

1947– Mededel. van de Bryol. Werkgroep van de Ned. Nat. Hist. Ver. Vol. 5 in 1951. Ed., E. Agsteribbe, Amsterdam.

Campbell, Douglas Houghton

1940. The Evolution of the Land Plants (Embryophyta). ix + 731 pp. Stanford: Stanford Univ. Press.

Camus, F.

1903. Notice sur M. Ém. Bescherelle. Bull. Soc. Bot. France, 50:227–239.

Cardot, Jules

1892. Monographie des Fontinalacées. Mém. Soc. Natl. Sci. Nat. Cherbourg, 28:1–152.

1905. Mousses de l'île Formose. Beih. Bot. Centr., 19(pt. 2):85–148.

1908. La flore bryologique des Terres Magellaniques, de la Géorgie du Sud et de l'Antarctide. Wiss. Ergeb. Schwed. Südpolar-Exped. 1901–1903, 4(pt. 8):1–298.

1913. Mousses. Deuxième Expédition Antarctique française (1908–1910) commandée par le Dr. Jean Charcot. 31 pp. Paris: Masson et cie.

Cardot, Jules, and Viktor F. Brotherus

1923. Les Mousses. Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. K. Svensk. Vet.-Akad. Handl., 63 (pt. 10):1–74.

Cardot, Jules, and Irénée Thériot

1902. The mosses of Alaska. Proc. Wash. Acad. Sci., 4:293–372. Reprinted in Harriman Alaska Expedition, 5:251–328 (1910).

Carl, Helmut

1931. Die Arttypen und die systematische Gliederung der Gattung Plagiochila Dum. Ann. Bryol., suppl. vol. 2, pp. i–viii, 1–170.

Casares-Gil, Antonio

1919. Flora Ibérica. Briófitas (1 pte.), Hepáticas. xx + 775 pp. Madrid: Mus. Nac. Cienc. Nat.

1932. Flora Ibérica. Briófitas (2 pte.), Musgos. xxx + 434 pp. Madrid: Mus. Nac. Cienc. Nat.

Castle, H.

1950. A revision of the genus *Radula*. Pt. II. Bryologist, 53:253–275.

Chalaud, G.

1945. Sur la place des Sphaignes dans la classification. Rev. Bryol. et Lichénol., n.s., 15:46–58.

Chen, P.-C.

1941. Studien über die ostasiatischen Arten der Pottiaceae. I, II. Hedwigia, 80:1–76, 141–322.

Chopra, Ram Saran

1943. A census of Indian hepatics. Journ. Indian Bot. Soc., 22:237–260.

Church, A. H.

1919. Thalassiophyta and the Subaerial Transmigration. 95 pp. Oxford: Oxford Univ. Press.

Clark, Lois, and Theodore C. Frye

1928. The liverworts of the Northwest. Publ. Puget Sound Biol. Sta., 6:1–194.

Conard, Henry S.

1944. How to Know the Mosses. Pictured-Keys for Determining Many of the North American Mosses and Liverworts, with Suggestions and Aids for Their Study. 166 pp. Mt. Pleasant, Iowa: H. E. Jaques.

Correns, Carl

1899. Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge. xxiv + 472 pp. Jena: G. Fischer.

Cortés Latorre, Cayetano

1951. Aportaciones a la briología española. Anal. Jard. Bot. Madrid, 10:261–300.

Crum, Howard A.

1951a. The Appalachian-Ozarkian Element in the Moss Flora of Mexico, with a Check-List of All Known Mexican Mosses. 504 pp. Ann Arbor, Mich.: Univ. Microfilms.

1951b. A checklist of mosses of northeastern Mexico. Soc. Bot. Mexico Bol., 12:1–27.

1952a. A preliminary survey of the Nicaraguan moss flora. Bryologist, 55:157–165.

1952b. Mosses from Honduras, II. Bryol., 55:279–285.

Crum, Howard A., and William Campbell Steere

1950. Additions to the moss flora of Panama. Bryologist, 53:139–152.

Cufodontis, G.

1951. Vorläufige Aufzählung der Laubmoose Äthiopiens. Oesterr. Bot. Zeitschr., 98:217–244.

Degenkolbe, W.

1937. Brutorgane bei beblätterten Lebermoosen. Ann. Bryol., 10:43–96.

Demaret, F.

1940. Prodrome des bryophytes du Congo belge et du Ruanda-Urundi. I. Musci. Bull. Jard. Bot. Bruxelles, 16:21–104.

1945. Prodrome des Mousses de Belgique. Bull. Jard. Bot. Bruxelles, 17:317–387.

Demaret, F., and R. Potier de la Varde

1951. Les espèces africaines du genre *Cyclodictyon* Mitt. Bull. Jard. Bot. Bruxelles, 21:11–59.

De Notaris, G.

1869. Epilogo della briologia italiana. Atti. R. Univ. Genova, 1:i–xxiv, 1–781.

Dixon, Hugh Neville

1913–1929. Studies in the bryology of New Zealand with special reference to the herbarium of Robert Brown, of Christchurch, New Zealand. N. Zealand Inst. Bull., 3:1–372, i–xviii.

1927. Gilbert Islands mosses. Journ. Bot., 65:254–257.

1929. On a small collection of mosses from the Seychelles. Ann. Bryol., 2:5–9.

1932. Contributions to the moss flora of Sumatra. Ann. Bryol., 5:17–50.

1934. Mosses of Celebes. Ann. Bryol., 7:19–36.

1935. Further contributions to the moss flora of Siam. Journ. Siam Soc. Nat. Hist. Suppl., 10 (pt. 1) :1–30.

1937. Mosses collected in Assam. Journ. Bombay Nat. Hist. Soc., 39:769–795.

1938. Tropical East African mosses. Pt. I. Acrocarpi. Journ. Bot., 76:217–228, 249–261.

1939. Mosses. *In* R. A. Dyer, The Flora of Tristan da Cunha: H.M.S. "Carlisle" Expedition, 1937. Bothalia, 3:598–601.

Dixon, Hugh Neville, and H. G. Jameson

1924. The Student's Handbook of British Mosses. 3rd ed. xlviii + 582 pp. Eastbourne: V. V. Sumfield.

Doignon, Pierre

1949. La régénération naturelle du peuplement muscinal dans les parcelles brûlées de la Forêt de Fontainebleau. Rev. Bryol. et Lichénol., n.s., 18:160–168.

Dombrowski, Gertrud

1933. Zur experimentellen Oekologie und Physiologie der Sporenverbreitung bei Laubmoosen. Bot. Archiv, 35:77–133.

Domin, Karel

1923. Grundzüge zur pflanzengeographischen Verbreitung und Gliederung der Lebermoose. Mém. Soc. Roy. Sci. Bohême, 1923 (pt. 8):1–74.

Döpp, W., and Ae. Döpp

1937. Bericht über einige neuere karyologische Arbeiten an Moosen. Ann. Bryol., 9 (1936):142–152.

Dugas, Marguerite

1928. Contribution a l'étude du genre "Plagiochila." Thèses présentées à la Faculté des Sciences de Paris. 199 pp. Paris: Masson et cie.

Dunham, Elizabeth Marie

1951. How to Know the Mosses. A Popular Guide to the Mosses of the Northwestern United States. 2nd ed. xxv + 289 pp. Boston: Mosher Press.

Du Rietz, G. Einar

1940. Problems of bipolar plant distribution. Acta Phytogeog. Suecica, 13:215–282.

1949. Huvudenheter och huvudgränser i svensk myrvegetation ("Main units and main limits in Swedish mire vegetation"). Svensk Bot. Tidskr., 43:274–309.

Eifrig, H.

1937. Monographische Studien über die indomalayischen Arten von Taxilejeunea. Ann. Bryol., 9 (1936):73–114.

Ernst-Schwarzenbach, Marthe

1944. La sexualité et le dimorphisme des spores des Mousses. Rev. Bryol. et Lichénol., n.s., 14:105–113.

Evans, Alexander W.

1911. The Hepaticae of the Bahama Islands. Bull. Torrey Club, 38:205–222.

1930. The thallose Hepaticae of the Juan Fernández Islands. *In* Skottsberg, Natural History of Juan Fernandez and Easter Island, 2:551–586.

1934. A revision of the genus *Acromastigum*. Ann. Bryol., suppl. vol. 3, pp. i–viii, 1–178.

1939. The classification of the Hepaticae. Bot. Rev., 5:49–96.

Evans, Alexander W., and George E. Nichols

1908. The bryophytes of Connecticut. Conn. Geol. and Nat. Hist. Surv. Bull., 11:1–203.

Fleischer, Max

1904–1924. Die Musci der Flora von Buitenzorg (zugleich Laubmoosflora von Java). 4 vols. Leiden: E. J. Brill.

1920. Natürliches System der Laubmoose. Hedwigia, 61:390–400.

1922. Kritische Revision der Carl Müllerschen Laubmoosgattungen. Hedwigia, 63: 209–216.

1929. Viktor-Ferdinand Brotherus. 1849–1929. Rev. Bryol., n.s., 2:71–81.

Flowers, Seville

1952. Monograph of the genus *Anacolia*. Bull. Torrey Club, 79:161–185.

Freitas, S. de

1948. Contribuçãs para o estudo das Hepáticas em Portugal. Brotéria, 17:146–171.

Fritsch, K.

1929. Die systematische Gruppierung der Bryophyten. Ber. Deutsch. Bot. Ges., 47: 614–618.

Frye, Theodore C., and Lois Clark

1937–1947. Hepaticae of North America. 5 pts., 1,018 pp. Seattle, Wash.: Univ. Washington Press.

FULFORD, MARGARET

1945. Studies on American Hepaticae. VI. Ceratolejeunea. Brittonia, 5:368–403.

1946. The genus *Bazzania* in Central and South America. Ann. Cryptogam. et Phytopathol., 3:i–xv, 1–75.

1948. Recent interpretations of the relationships of the Hepaticae. Bot. Rev., 14: 127–173.

1951. Distribution patterns of the genera of leafy Hepaticae of South America. Evolution, 5:243–264.

FULFORD, MARGARET, GLADYS CARROLL, and THOMAS J. COBBE

1947. The response of *Leucolejeunea clypeata* to variations in the nutrient solution. Bryologist, 50:113–146.

FULFORD, MARGARET, and HAROLD KERSTEN

1947. The reaction of *Leucolejeunea clypeata* to variations in dosage of soft X rays. Bryologist, 50:147–156.

GAMS, HELMUT

1934. Beiträge zur Kenntnis der Steppenmoose. Ann. Bryol., 7:37–56.

1950. Kleine Kryptogamenflora von Mitteleuropa. I: Die Moos und Farnpflanzen (Archegoniaten). 3rd ed. 186 pp. Jena: G. Fischer.

GATTEFOSSE, J., and R. G. WERNER

1932. Catalogus bryophytorum marocanorum adhuc cognitorum. Bull. Soc. Sci. Nat. Maroc, 12:228–280.

GIACOMINI, V.

1947. Syllabus Bryophytarum Italicarum. Pars Prima: Andreaeales et Bryales. Atti, Ist. Bot. Univ. Pavia, Labor. Crittogam., ser. 5, 4:179–292.

GIMINGHAM, C. H., and E. T. ROBERTSON

1950. Preliminary investigations on the structure of bryophytic communities. Trans. British Bryol. Soc.

GJAERVOLL, O.

1950. The snow-bed vegetation in the surroundings of Lake Torneträsk, Swedish Lappland. Svensk. Bot. Tidskr., 44:387–440.

GOEBEL, KARL

1930–1933. Organographie der Pflanzen inbesondere der Archegoniaten und Samenpflanzen. 3rd ed. 2 vols. Jena: G. Fischer.

GOTTSCHE, C. M.

1867. De mexikanske Levermosser. Vidensk.-Selsk. Skr., V Raekke, naturvid.-math. Afdeln., 6:99–381.

GOTTSCHE, C. M., J. B. G. LINDENBERG, and C. G. NEES AB ESENBECK

1844–1847. Synopsis Hepaticarum. xxvi + 834 pp. Hamburg: Meissner.

GRIGGS, ROBERT F.

1934. Growth of liverworts from Katmai in nitrogen-free media. Amer. Journ. Bot., 21:265–277.

1935. Hepaticae as pioneers on nitrogen-free volcanic ash. Ann. Bryol., 8:74–79.

GROUT, ABEL JOEL

1898. A list of the mosses of Vermont with analytical keys to the genera and species. Contr. Bot. Vermont, Bot. Dept., Univ. Vermont, 1:1–39.

1903–1908. Mosses with hand-lens and microscope. A non-technical hand-book of the more common mosses of the Northeastern United States. 416 pp. New York: Mount Pleasant Press.

Grout, Abel Joel (Cont.)

1916. The Moss Flora of New York City and vicinity. 119 pp. New Dorp, New York: Publ. by author.

1928–1940. Moss Flora of North America, North of Mexico. 3 vols. Newfane, Vermont: Publ. by author.

1945. A revision of the North American species of Stereophyllum and Pilosium, with descriptions of some South American species. Bryologist, 48:60–70.

1947. Mosses with a Hand-Lens. A Popular Guide to the Common or Conspicuous Mosses and Liverworts of the United States and Canada. 4th ed. xiv + 344 pp. Newfane, Vermont: Publ. by author.

Hagerup, O.

1935. Zur Periodizität im Laubwechsel der Moose. K. Dansk. Vidensk. Selsk. Biol. Meddel., 11(pt. 9):1–88.

Harris, Thomas M.

1938. The British Rhaetic Flora. xi + 84 pp. London: British Museum.

1939. Naiadita, a fossil bryophyte with reproductive organs. Ann. Bryol., 12:57–70.

Haskell, G.

1949. Some evolutionary problems concerning the Bryophyta. Bryologist, 52:49–57.

Hattori, Sinske

1951. On the distribution of the Hepaticae of Shikoku and Kiushiu (Southern Japan). Bryologist, 54:103–118.

Haupt, Gertraud

1932, 1933. Beiträge zur Zytologie der Gattung Marchantia (L.). I, II. Zeitschr. f. indukt. Abstammungs- u. Vererbungslehre, 62:367–428; 63:290–419.

Hedwigia

1852–1944. Organ für Kryptogamenkunde und Phytopathologie nebst Repertorium für Literatur. Vols. 1–81. Ed., Dr. H. Reimers. Berlin-Dahlem.

Heitz, Emil

1942. über die Beziehung zwischen Polyploidie und Gemischtgeschlechtlichkeit bei Moosen. Arch. Julius Klaus-Stiftung f. Vererbungsf. Sozialanthro. u. Rassenhygiene, 17:444–448.

1945. Moosmutationen I. Spontane und durch Colchicin ausgelöste polyploide Mutanten bei *Aulacomnium androgynum* (L.). Arch. Julius Klaus-Stiftung f. Vererbungsf. Sozialanthro. u. Rassenhygiene, 20 (Ergänzungsband):119–125.

Henderson, Nellie F.

1927–1931. Ohio mosses. Ohio Journ. Sci. Vols. 25, 27, 29, 31.

Herter, W. G.

1933. Florula uruguayensis. Plantae Avasculares. Musci. Ostenia (Colección de trabajos botánicos dedicados a Don Cornelio Osten), 1933:50–56.

Herzog, Th.

1916, 1920. Die Bryophyten meiner zweiten Reise durch Bolivia. Bibl. Bot., 87:1–347; 88:1–31.

1925. Anatomie der Lebermoose. *In* Linsbauer, Handbuch der Pflanzenanatomie. Vol. 12, Lieferung 12, pp. i–iv, 1–112.

1926. Geographie der Moose. xi + 439 pp. Jena: G. Fischer.

1932, 1938. Beiträge zur Kenntnis der Gattung Plagiochila. I, II. Hedwigia, 72:195–242; 78:222–244.

1939. Studien über Drepanolejeunea. IV. Ann. Bryol., 12:98–122.

HERZOG, TH. (Cont.)

1942. Die foliosen Lebermoose der Juan Fernández-Inseln und der Osterinsel. *In* Skottsberg, Natural History of Juan Fernandez and Easter Island. 2:697–752.

1950. Hepaticae Borneenses (Oxford University Expedition to Sarawak, 1932). Trans. British Bryol. Soc., 1(pt. 4):275–329.

1951. Hepaticae Standleyanae Costaricenses et Hondurenses. Pars. II. Rev. Bryol. et Lichénol., n.s., 20:126–175.

HESSELBO, AUG.

1918. The Bryophyta of Iceland. *In* Rosenvinge and Warming, The Botany of Iceland, 1:395–675.

1924. Bryophyta. *In* Gandrup, A botanical trip to Jan Mayen. Dansk Bot. Arkiv., 4(pt. 5):28–34.

1937. Mosses collected on the Fifth Thule Expedition. Report of the Fifth Thule Expedition 1921–24, 2(pt. 2):1–17.

HODGSON, E. A.

1950. The classification of New Zealand Hepaticae. Tuatara, 3:20–32.

HOFFMANN, G.

1935. Monographische Studien über die Indomalayischen Arten von Pycnolejeunea. Ann. Bryol., 8:80–129.

HOFLEUR, K.

1942. Über die Austrocknungsfähigkeit des Protoplasmas. Ber. Deutsch. Bot. Ges., 15:94–107.

HOFMEISTER, W.

1851. Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen. 179 pp. Leipzig.

HORIKAWA, YOSHIWO

1934. Monographia Hepaticarum australi-japonicarum. Journ. Sci., Hiroshima Univ., ser. B, Div. II, 2:101–325.

1950–. Enumeratio Bryophytarum Archipelago-japonicarum. Journ. Sci., Hiroshima Univ., ser. B, div. 2, 6:11–25.

HOWE, MARSHALL A.

1899. The Hepaticae and Anthocerotes of California. Mem. Torrey Club, 7:1–208.

HUSNOT, T.

1884–1890. Muscologia Gallica. Description & figures des mousses de France et des contrées voisines. 2 vols. Cahan, par Athis: T. Husnot.

1893. Nécrologie. M. Charles Maurice Gottsche. Rev. Bryol., 20:46–48.

1911. Nécrologie. Le Général Paris. Rev. Bryol., 38:93–95.

1922. Hepaticologia Gallica. Flore analytique et descriptive des hépatiques de France et des contrées voisines. 163 pp. Cahan, par Athis: T. Husnot.

IISHIBA, EIKICHI

1929, 1939. General Study of Japanese Mosses. 2 vols. Tokyo.

1931. Species Hepaticarum Nipponicarum. 95 pp. Sendai: Shokubutsu Doshikai.

IRMSCHER, EDGAR

1929. Pflanzenverbreitung und Entwicklung der Kontinente. Teil II. Weitere Beiträge zur genetischen Pflanzengeographie unter besonderer Berücksichtigung der Laubmoose. Mitteil. Inst. Allegem. Bot. Hamburg, 8(Heft 1):169–374.

JACHIMSKY, H.

1935. Beitrag zur Kenntnis von Geschlechtschromosomen und Heterochromatin bei Moosen. Jahrb. Wiss. Bot., 81(pt. 2):203–238.

Jaeger, August, and Fr. Sauerbeck

1870–1880. Genera et species muscorum systematice disposita seu adumbratio florae Muscorum totius orbis terrarum. Ber. St. Gall. Naturwiss. Ges. Vols. 1869–70 to 1878–79. (Also published separately in 2 vols., with separate pagination.)

Jäggli, Mario

1935. Leopold Loeske (1865–1935). Rev. Bryol. et Lichénol., n.s., 8:137–142.

Jalas, Jaakko

1950. Zur Kausalanalyse der Verbreitung einiger nordischen Os- und Sandpflanzen. Ann. Bot. Soc. Zool. Bot. Fennicae "Vanamo," 24:i–xii, 1–362.

Jedlička, J.

1948. Monographia specierum europaearum gen. Plagiothecium s.s. Partis specialis I. Summarium. Publ. Fac. Sci., Masaryk Univ. No. 308, pp. 1–45.

Jennings, O. E.

1951. A Manual of the Mosses of Western Pennsylvania and Adjacent Regions. 2nd ed. Amer. Midl. Nat. Monogr., Vol. 6, 396 pp.

Jensen, C.

1915, 1923. Danmarks Mosser eller beskrivelse af de i Danmark med Faerøerne Fundne Bryofyter. I. Hepaticales, Anthocerotales og Sphagnales. II. Andreaeales og Bryales. 2 vols. København: Gyldendalske Boghandel.

1939. Skandinaviens Bladmossflora. 535 pp. København: Ejnar Munksgaard.

Jones, George Neville

1930. The moss flora of southeastern Washington and adjacent Idaho. Res. Studies State Coll. Washington, 1:113–192.

Jørgensen, E.

1934. Norges Levermoser. Bergens Mus. Skr., 16:1–343.

Journal of the Hattori Botanical Laboratory

1947– Ed., Sinske Hattori, Kyushu, Japan.

Jovet, Suzanne, and Paul Jovet

1944. Peuplement bryologique des bois pourrissants et rochers ombragés des environs de Samoëns (Haute-Savoie). Rev. Bryol. et Lichénol., n.s., 14:120–148.

Jovet-Ast, Suzanne

1948a. Les hépatiques de Madagascar. Mém. Inst. Sci., Madagascar, sér. B, 1:39–42.

1948b. Les mousses et les sphaignes de Madagascar. Mém. Inst. Sci., Madagascar, sér. B, 1:43–56.

Juratzka, Jakob

1882. Die Laubmoosflora von Oesterreich-Ungarn. Zusammengestellt von J. Breidler und J. B. Förster. x + 385 pp. Wien: W. Braumüller.

Kabiersch, W.

1936, 1937. Studien über die ostasiatischen Arten einiger Laubmoosfamilien. I, II. Hedwigia, 76:1–94; 77:71–136.

Kashyap, Shiv Ram

1929, 1932. Liverworts of the Western Himalayas and the Panjab Plain. 2 vols. Lahore, India: Univ. Panjab.

Keever, Catherine, Henry J. Oosting, and Lewis E. Anderson

1951. Plant succession on exposed granite of Rocky Face Mountain, Alexander County, North Carolina. Bull. Torrey Club, 78:401–421.

Koppe, F.

1931. Beobachtungen über Frostschaden an Moosen. Ber. Deutsch. Bot. Ges., 49:35–51.

Kühnemann, O.

1938. Catálogo de los musgos argentinos. Lilloa, 2:37–183.

Kurz, H., and T. M. Little

1933. Liverworts of north and central Florida. Bull. Florida State Coll. for Women, 26:1–39.

Lange, Joh., and C. Jensen

1887. Oversigt over Grønlands Mosser. Meddelel. om Grønland, 3:1–110.

La Rue, Carl D.

1942. The effect of wounding, of wound hormones and of growth hormones on rhizoid formation in mosses and liverworts. Bryologist, 45:35–39.

Latzel, A.

1931. Vorarbeiten zu einer Laubmoosflora Dalmatiens. Beih. Bot. Centr., 48:437–512.

Lazarenko, A. S.

1951. Opredelitel' listvennykh mkhov BSSR [A key to the leafy mosses of White Russia]. 397 pp. Minsk: Akad. Nauk Belorusskoi SSR.

Leitgeb, H.

1874–1881. Untersuchungen über die Lebermoose. 6 vols. Jena, Graz.

Lesquereux, Leo, and Thomas P. James

1884. Manual of the Mosses of North America. v + 447 pp. Boston: S. E. Cassino.

Lid, Johannes

1924. Sphagna from Novaya Zemlya, with an appendix by E. Jørgensen: Some Mosses from Novaya Zemlya. Report . . . of the Norwegian Expedition to Novaya Zemlya, 1921. No. 20, pp. 1–7.

1941. Bryophytes of Jan Mayen. Norges Svalbard- og Ishavs-Undersøkelser, Meddelelse. No. 48, pp. 1–13.

Limpricht, K. Gustav

1885–1903. Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. Unter Berücksichtigung der übrigen Länder Europas u. Sibiriens. 3 vols. Leipzig: E. Kummer.

Lindberg, S. O., and H. Wilh. Arnell

1889–1890. Beschreibung der von den schwedischen Expeditionen nach Sibirien in den Jahren 1875 und 1876 gesammelten Moose mit Berücksichtigung aller früheren bryologischen Angaben für das russische Nord-Asien. I. Lebermoose. II. Laubmoose. K. Svensk. Vet.-Akad. Handl., 23(pt. 5):1–69; (pt. 10):1–163.

Loeske, Leopold

1910. Studien zur vergleichenden Morphologie und phylogenetischen Systematik der Laubmoose. 224 pp. Berlin: M. Lande.

1929. Die Laubmoose Europas. II. Funariaceae. viii + 120 pp. Berlin-Schöneberg: M. Lande.

1930. Monographie der europäischen Grimmiaceen. Bibl. Bot., 101:i–ix, 1–236.

1935. Bemerkungen zur Systematik der Laubmoose. Ann. Bryol., 8:130–149.

Lorch, Wilhelm

1931. Anatomie der Laubmoose. *In* Linsbauer, Handbuch der Pflanzenanatomie, 7 (Lieferung 28):i–viii, 1–359.

LOWRY, ROBERT J.

1948. A cytotaxonomic study of the genus Mnium. Mem. Torrey Club, 20: (pt. 2):1–42.

LUISIER, A.

1927–1945. Les mousses de l'Archipel de Madère et en général des Iles Atlantiques. Brotéria. Ann. vols., 1927–1945.

LUTHER, HANS

1951. Verbreitung und ökologie der höheren Wasserpflanzen im Brackwasser der Ekenäs-Gegend in Südfinnland. Acta Bot. Fennica. Vols. 49, 50.

MACOUN, JOHN, and NILS C. KINDBERG

1892, 1902. Catalogue of Canadian Plants. Pt. VI, Musci. v + 295 pp. Montreal: William Foster Brown. Pt. VII, Lichenes and Hepaticae. xix + 318 pp. Ottawa: Govt. Printing Bureau.

MACVICAR, SYMERS M.

1926. The Student's Handbook of British Hepatics. 2nd ed. xxxi + 464 pp. Eastbourne: V. V. Sumfield.

MÄGDEFRAU, K.

1938. Der Wasserhaushalt der Moose. Ann. Bryol., 10(1937):141–150.

MÄGDEFRAU, K., and A. WUTZ,

1951. Die Wasserkapazität der Moos- und Flechtendecke des Waldes. Forstwiss. Centr., 70:103–117.

MALTA, N.

1926. Die Gattung Zygodon Hook. et Tayl. Eine monographische Studie. Latvi. Univ. Bot. Darza Darbi, 1:1–184.

1931. Übersicht der Moosflora des Ostbaltischen Gebietes. II. Laubmoose. Acta Hort. Bot. Univ. Latvien., 5:75–184.

1933. A survey of the Australasian species of Ulota. Acta Hort. Bot. Univ. Latvien., 7:1–24.

1936. Monographic work in bryology. Proc. 6th Internat. Congr. Bot., 1:318–320.

MARCHAL, ÉL., and ÉM. MARCHAL

1911. Aposporie et sexualité chez les Mousses. Bull. Acad. Roy. Belgique, Cl. Sci., 1911:750–776.

MEIJER, WILLEM

1950. Over de Waarde van de Bryologie bij het Onderzoek van subfossiele Veenlagen. Buxbaumia, 4:13–15.

1951. The genus *Orthodontium*. Academ. Proefschr. xiii + 80 pp. Amsterdam: North-Holland Publ. Co.

MEUSEL, H.

1935. Wuchsformen und Wuchstypen der europäischen Laubmoose. Nova Acta Leopold., n.s., 3(pt. 12):123–277.

MEYER, SAMUEL LEWIS

1941. Physiological studies on mosses. II. Spore longevity in *Physcomitrium turbinatum* and *Funaria hygrometrica*. Bryologist, 44:69–75.

MEYER, SAMUEL LEWIS, and C. H. FORD

1943. Influence of the Hydrogen-ion concentration of the substrate on the development of leafy moss plants. Plant Physiol., 18:530–533.

MEYLAN, CHARLES

1924. Les Hépatiques de la Suisse. Beitr. Kryptogam. flora Schweiz, 6(pt. 1):1–318.

1940. Contribution à la connaissance de la flore bryologique de l'Islande. Bull. Soc. Bot. Suisse, 50:475–499.

MITTEN, WILLIAM

1859. Musci indiae orientalis; an enumeration of the mosses of the East Indies. Journ. and Proc. Linn. Soc. Bot., 1(suppl.):1–171.

1869. Musci austro-americani. Enumeratio muscorum omnium austro-americanorum auctori hucusque cognitorum. Journ. Linn. Soc. Bot., 12:1–659.

MÖLLER, HJALMAR

1911–1936. Löfmossornas Utbredning i Sverige. Arkiv Bot., Vols. 10–28.

MÖNKEMEYER, WILH.

1927. Die Laubmoose Europas. IV. Ergänzungsband. Andreaeales-Bryales. x + 960 pp. Leipzig: Akadem. Verlagsges.

MORRILL, JOHN B.

1950. Mosses in liquid air. Bryologist, 53:163–164.

MÜLLER, CARL

1848–1851. Synopsis Muscorum Frondosorum Omnium Hucusque Cognitorum. 2 vols.. Berlin: Alb. Foerstner.

1901. Genera Muscorum Frondosorum. vi + 474 pp. Leipzig: E. Kummer.

MÜLLER, KARL

1905–1916. Die Lebermoose Deutschlands, Oesterreichs u. d. Schweiz mit Berücksichtigung der übrigen Länder Europas. 2 vols. Leipzig: E. Kummer.

1905. Monographie der Lebermoosgattung Scapania Dum. Nova Acta. Abh. K. Leop.-Carol. Deutsch. Akad. Naturf., 83:1–312.

1948a. Der systematische Wert von Sporophytenmerkmalen bei den beblätterten Lebermoosen. Svensk Bot. Tidskr., 42(pt. 1):1–16.

1948b. Hepaticae Latzelianae III. Weiterer Beitrag zur Kenntnis der Lebermoosflora Dalmatiens und der Herzegowina. Oesterr. Bot. Zeitschr., 94:330–347.

1951. Die Lebermoose Europas (Musci hepatici). 3rd ed. Lieferung 1, 2, pp. 1–320. Leipzig: Akadem. Verlagsges.

NANNFELDT, JOHN AXEL, and G. EINAR DU REITZ

1945. Vilda Växter i Norden: Mossor, Lavar, Svampar, Alger. xlviii + 433 pp. Stockholm: Bokförlaget Natur och Kultur.

NICHOLS, GEORGE E.

1938. Alexander William Evans, hepaticologist. Ann. Bryol., 11:1–5.

NICHOLSON, WILLIAM E.

1907. William Mitten. A sketch with bibliography. Bryologist, 10:1–5.

NICHOLSON, WILLIAM E., TH. HERZOG, and FRANS VERDOORN

1930. Hepaticae. *In* H. Handel-Mazzetti, Symbolae Sinicae, 6:1–60.

PAGÁN, FRANCISCO M.

1939. A preliminary list of the Hepaticae of Puerto Rico including Vieques and Mona Island. Bryologist, 42:1–12, 37–50, 71–82.

1942. Catalogue of the Hepaticae of Guadeloupe. Bryologist, 45:76–110.

PARIS, E. G.

1903–1906. Index Bryologicus sive Enumeratio Muscorum ad Diem Ultimam Anni 1900 Cognitorum. 2nd ed. 5 vols Paris: A. Hermann.

1908. Florule bryologique de la Guinée française. Mem. Soc. Bot. France, 47:1–66.

PATTERSON, PAUL M.

1943. Some ecological observations on bryophytes. Bryologist, 46:1–13.

1946. Osmotic values of bryophytes and problems presented by refractory types. Amer. Journ. Bot., 33:604–611.

PAUL, H.

1924. Sphagnaceae (Torfmoose). *In* Engler and Prantl, Die natürlichen Pflanzenfamilien. 2nd ed., 24:105–125.

PEARSON, WILLIAM HENRY

1902. The Hepaticae of the British Isles; Being Figures and Descriptions of All Known British Species. 2 vols. London: L. Reeve and Co.

PERSSON, HERMAN

1942. Arctic bryophytes mainly collected by the Rev. J. Lagerkranz. Svensk Bot. Tidskr., 36:444–450.

1944a. Existence de Mousses au fond des lacs en Suède. Rev. Bryol. et Lichénol., n.s., 13:84–88.

1944b. On some species of Aloina, with special reference to their dispersal by the wind. Svensk Bot. Tidskr., 38:260–268.

1948. On the discovery of *Merceya ligulata* in the Azores with a discussion of the so-called "copper mosses." Rev. Bryol. et Lichènol., 17:75–78.

1952. Additional list of Alaska-Yukon mosses. Bryologist, 55:261–279.

PHILLIPS, EDWIN A.

1951. The associations of bark-inhabiting bryophytes in Michigan. Ecol. Monogr., 21:301–316.

PICCIOLI, ELIVIRA

1932. Les espèces européennes du genre *Orthotrichum*. Trav. Inst. Bot. Univ. Neufchâtel, n.s., 1:1–128.

PILOUS, ZDENEK

1948. Naše Mechy. Illustrovany Kliě Kurčovani mechu československych. 326 pp. Praha.

PITTIER, HENRI

1936. Los musgos de Venezuela. Bol. Soc. Venez. Cienc. Nat. 3(no. 27):353–389.

PODPĚRA, JOSEF

1942–1951. Bryum generis monographiae prodromus. Pars 1–5. Acta Soc. Sci. Nat. Moravicae. Vols. 14–23.

POLUNIN, NICHOLAS

1948. Hepaticae. *In* Botany of the Canadian Eastern Arctic. Nat. Mus. Canada Bull., 97:491–512.

POTIER DE LA VARDE, R.

1928. Mousses de l'Oubangui. Arch. Bot., Vol. 1 (1927), mém. 3, pp. 1–152.

1936. Mousses du Gabon. Mém. Soc. Nation. Sci. Nat. et Math. Cherbourg, 42:1–270.

1948. Irénée Thériot (21 décembre 1859—25 mars 1947). Rev. Bryol. et Lichénol., n.s., 17:7–14.

POTZGER, JOHN E.

1939. Microclimate, evaporation stress, and epiphytic mosses. Bryologist, 42:53–61.

PRINGSHEIM, N.

1878. Ueber Sprossung der Moosfrüchte und den Generationswechsel der Thallophyten. Jahrb. Wiss. Bot., 11:1–46.

REIMERS, H.

1931. Beiträge zur Moosflora Chinas I. Hedwigia, 71:1–71.

1933. Revision der Lebermoosga**ung Micropterygium. Hedwigia, 73:133–204.

REIMERS, H. (Cont.)

1937. Die europäischen Haplocladium-Arten mit besonderer Berücksichtigung ihrer aussereuropäischen Verbreitung und ihrer Verwandtschaft. Hedwigia, 76: 191–298.

RENAULD, F., and JULES CARDOT

1915. Histoire naturelle des plantes: Mousses. *In* Grandidier, Histoire physique, naturelle et politique de Madagascar. Vols. 29, 30. Paris: Imprimerie Nationale.

REVUE BRYOLOGIQUE ET LICHÉNOLOGIQUE

1874– Directeur, Mme. P. Allorge, Mus. Natl. Hist. Nat. Paris. Vol. 20, n.s., in 1951.

RICHARDS, PAUL W.

1934. Musci collected by the Oxford Expedition to British Guiana in 1929. Roy. Bot. Gard. Kew Bull. Misc. Info., 8:317–337.

1940. Literature on the ecology of bryophytes published since 1932. Journ. Ecol., 28:245–248.

1950. A Book of Mosses. 40 pp., 16 col. pls. London: Penguin Books.

RINK, W.

1935. Zur Entwicklungsgeschichte, Physiologie und Genetik der Lebermoosgattung Anthoceros und Aspiromitus. Flora, 130:87–130.

ROBERTS, EDITH A., and INEZ M. HARING

1938. The water relations of the cell walls of certain mosses as a determining factor in their distribution. Ann. Bryol., 10(1937):97–114.

RODGERS, ANDREW DENNY

1940. "Noble Fellow." William Starling Sullivant. xxii + 361 pp. New York: Putnam.

ROIVAINEN, H., and EDWIN B. BARTRAM

1937. Bryological investigations in Tierra del Fuego. Ann. Bot. Soc. Zool.-Bot., Fennicae, "*Vanamo*," 9(no. 2):i–x, 1–58.

ROMOSE, VAGN

1940. ökologische Untersuchungen über *Homalothecium sericeum*, seine Wachstumsperioden und seine Stoffproduktion. Dansk. Bot. Archiv., 10(pt. 4):1–134.

ROTH, GEORG

1904–1905. Die Europäischen Laubmoose beschrieben und gezeichnet. 2 vols. Leipzig: W. Engelmann.

1911. Die aussereuropäischen Laubmoose. x + 331 pp. Dresden: C. Heinrich.

SAINSBURY, G. O. K.

1952. Vegetative reproduction in New Zealand mosses. III. Bryologist, 55:71–79.

SANBORNE, ETHEL I.

1929. Hepaticae and Anthocerotes of western Oregon. Univ. Oregon Publ. Plant Biol., 1:1–111.

SAVICZ, LYDIA

1924. Ueber die neuen Fundorte der Mooses in arktischen Sibirien. Not. System. Inst. Cryptogam. Hort. Bot. Petropolitani.

1936a. Les mousses de l'Archipel François-Joseph, Severnaïa, Zemlia, île Wiese, récoltées par V. P. Savicz durant l'expédition polaire de 1930 sur le brise-glace "G. Sédov." Acta Inst. Bot. Acad. Sci. URSS, Ser. 2, fasc. 3, pp. 505–578.

1936b. Sphagnales Partis Europeae URSS. 104 pp. Moscow: Acad. Sci. URSS.

Savicz, Lydia, and K. I. Ladyzhenskaja

1936. Hepaticae Regionum septentrionalium Partis Europeae URSS. Moscow: Acad. Sci. URSS.

Schiffner, Victor

1893–1895. Hepaticae (Lebermoose). *In* Engler and Prantl, Die natürlichen Pflanzenfamilien. Teil 1, Abt. 3, pp. 3–141.

1898. Conspectus Hepaticarum Archipelagi Indici. 382 pp. Batavia: Staatsdrückerei.

1900. Die Hepaticae der Flora der Buitenzorg. 220 pp. Leiden: E. J. Brill.

1901–1937. Kritische Bemerkungen über die europäischen Lebermoose mit Bezug auf die Exemplare des Exsiccatenwerkes: Hepaticae europaeae exsiccatae; i–xxii ser. Wien: V. Schiffner.

1917. Die systematisch-phylogenetische Forschung in der Hepaticologie seit dem Erscheinen der Synopsis Hepaticarum und über die Abstammung der Bryophyten und Pteridophyten. Progressus Rei Bot., 5:387–520.

1929. Über epiphylle Lebermoose aus Japan nebst einigen Beobachtungen über Rhizoiden, Elateren und Brutkörper. Ann. Bryol., 2:87–106.

Schornherst, Ruth O.

1943. Phytogeographic studies of the mosses of Northern Florida. Amer. Midl. Nat., 29:509–532.

Schuster, Rudolf

1949. The ecology and distribution of Hepaticae in central and western New York. Amer. Midl. Nat., 42:513–712.

Sharp, Aaron J.

1939. Taxonomic and ecological studies of eastern Tennessee bryophytes. Amer. Midl. Nat., 21:267–354.

1944. Some problems in American bryology. Lilloa, Rev. Bot. Inst. Miguel Lillo, 10: 265–283.

Sherrin, William Robert

1927. An Illustrated Handbook of the British Sphagna (after Warnstorf). x + 74 pp. London: Taylor and Francis.

Sim, T. R.

1926. The Bryophyta of South Africa. Trans. Roy. Soc. South Africa, 15:1–475.

Sinoir, Yves

1952. Génétique et cytotaxonomie des bryophytes. Rev. Bryol. et Lichénol., 21:32–45.

Sjörs, Hugo

1948. Myrvegetation i Bergslagen. (Mire vegetation in Bergslagen, Sweden.) Acta Phytogeog. Suecica, 21:1–340.

Šmarda, Jan

1948. Mechy Slovenska. (The mosses of Slovakia, ČSR). Casopis Zemsnského Musea Ďrně, 32:1–75.

Smith, Gilbert Morgan

1938. Cryptogamic Botany. 2 vols. [New ed. in press.] New York: McGraw-Hill.

Sörensen, H.

1948. Studies on the ecology of Danish water and bog mosses. Dansk Bot. Arkiv, 12(pt. 10):5–47.

Springer, Eva

1935. Über apogame (vegetativ entstandene) Sporogone an der bivalenten Rasse des Laubmooses *Phascum cuspidatum.* Zeitschr. f. indukt. Abstammungs- u. Vererbungslehre, 69:249–262.

SPRUCE, RICHARD

1885. Hepaticae of the Amazon and of the Andes of Peru and Ecuador. Trans. and Proc. Bot. Soc. Edinburgh, 15:i–xi, 1–588.

STÅLFELT, M. G.

1937. Der Gasaustausch der Moose. Planta, 27:30–60.

STEERE, WILLIAM CAMPBELL

1937. *Bryoxiphium norvegicum*, the sword moss, as a preglacial and interglacial relic. Ecology, 18:346–358.

1938. Critical bryophytes from the Keweenaw Peninsula, Michigan. II. Ann. Bryol., 11:145–152.

1942. Pleistocene mosses from the Aftonian interglacial deposits of Iowa. Pap. Mich. Acad. Sci., Arts and Letters, 27(1941):75–104.

1945. Robert Statham Williams (1859–1945). Bryologist, 48:93–99.

1946a. Mosses of British Honduras and the Department of Petén, Guatemala. III. Bryologist, 49:72–84.

1946b. Cenozoic and Mesozoic bryophytes of North America. Amer. Midl. Nat., 36: 298–324.

1947. A consideration of the concept of genus in Musci. Bryologist, 50:247–258.

1948a. Abel Joel Grout (1867–1947). Bryologist, 51:201–212.

1948b. Musci. *In* Polunin, Botany of the Canadian Eastern Arctic. Nat. Mus. Canada, Bull., 97:370–490.

1948c. Contribution to the bryogeography of Ecuador. I. A review of the species of Musci previously reported. Bryologist, 51:65–167.

1950. Liverworts of Southern Michigan. 2nd ed. Cranbrook Inst. Sci. Bull., 17:1–97.

1951. Bryophyta of Arctic America. IV. The mosses of Cornwallis Island. Bryologist, 54:181–202.

STEERE, WILLIAM CAMPBELL, and DOROTHY E. CHAPMAN

1946. Mosses of El Salvador. Journ. Washington Acad. Sci., 36:219–225.

STEPHANI, FRANZ

1894. Richard Spruce. Bot. Centr., 57(pt. 12):370–374.

1898–1924. Species Hepaticarum sive Enumeratio Monographica Hepaticarum Orbis Terrarum Hucusque Cognitarum. 6 vols. Genève: Univ. Genève et Herbier Boissier.

1911. Die Lebermoose. Botanische Ergebnisse der Schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. K. Svensk. Vet.-Akad. Handl., 46 (pt. 9):1–92.

STEPPUTAT, W., and H. ZIEGENSPECK

1929. Morphologische Untersuchungen über die Phylogenie der Laubmoose. Bot. Archiv, 24:1–127.

STØRMER, PER

1940. Bryophytes from Franz Josef Land and eastern Svalbard. Norges Svalbard- og Ishavs-Undersøkelser, Meddelel., 47:1–16.

1946. Moser fra Skog og Myr. 111 pp., 29 pls. Oslo: Johan Grundt Tanum.

STRASBURGER, EDUARD

1894. The periodic reduction of the number of the chromosomes in the life-history of living organisms. Ann. Bot., 8:281–316.

SULLIVANT, WILLIAM S.

1856. The Musci and Hepaticae of the United States East of the Mississippi River Contributed to the Second Edition of Gray's Manual of Botany. iv + 113 pp. New York: Putnam.

SULLIVANT, WILLIAM S. (Cont.)

1864, 1874. Icones Muscorum, or Figures and Descriptions of Most of Those Mosses Peculiar to Eastern North America Which Have Not Been Heretofore Figured. viii + 216 pp. Supplement (posthumous). viii + 109 pp. Cambridge, Mass.: Sever and Francis.

TEODORESCO, E. C.

1929. Observations sur las croissance des plantes aux lumières de diverses longeurs d'onde. Ann. Sci. Nat. Bot., sér. 10, 11:201–336.

THÉRIOT, IRÉNÉE

1910. Biographical sketch of Monsieur Renauld. Liste des publications de M. F. Renauld. Bryologist, 13:113–116, 125–128.

1930. Le genre *Haplocladium* en Asie et en Afrique. Ann. Cryptogam. Exotique, 3:57–100.

1933. Mexican mosses. IV. Rev. Bryol. et Lichénol., n.s., 5(1932):91–110.

1935. Jules Cardot (1860–1934). Rev. Bryol. et Lichénol., n.s., 8:5–13.

1939–1941. Complément au Catalogue des Mousses de Cuba. Mem. Soc. Cubana de Hist. Nat. Felipe Poey. Vols. 13, 14. 15.

1944. Musci hispaniolensis. Trav. [Rev.] Bryol. et Lichénol., 14:7–25.

TRABUT, L.

1942. Flore des Hépatiques de l'Afrique du Nord. Mélanges [Rev.] Bryol. et Lichénol., 12:1–43.

TRANSACTIONS OF THE BRITISH BRYOLOGICAL SOCIETY

1947– F. A. Sowter, ed., Leicester, England. Preceded by: Annual Reports of the Moss Exchange Club, 1896–1922; and Annual Reports of the British Bryological Society, 1923–1946.

TUOMIKOSKI, RISTO

1949. Über die Kollektivart *Drepanocladus exannulatus* (Br. eur.) Warnst. Ann. Bot. Soc. Zool. Bot. Fennicae "Vanamo," 23(pt. 1):i–iv, 1–44.

URSING, BJÖRN

1949. Svenska Växter i Text och Bild. Kryptogamer. 529 pp. Stockholm: Nordisk Rotogravyr.

VAARAMA, ANTERO

1950. Studies on chromosome numbers and certain meiotic features of several Finnish moss species. Bot. Not., 1950:239–256.

VANDEN BERGHEN, C.

1949. Aperçu sur la biologie des Hépatiques épiphylles. Biol. Jaarb. Dodonaea, 1949: 215–221.

VANDEN BERGHEN, C., and P. DUVIGNEAU

1943. Catalogue des Hépatiques de la flore belge. Bull. Soc. Bot. Belgique, 75:87–99.

VERDOORN, FRANS

1930. Die Frullaniaceae der Indomalesischen Inseln. Ann. Bryol., suppl. vol. 1, pp. 1–187.

1931. Max Fleischer †. Ann. Bryol., 4:113–122.

1932. (Ed.) Manual of Bryology. ix + 486 pp. The Hague: M. Nijhoff.

1934. Studien über Asiatische Jubuleae (De Frullaniaceis XV–XVII). Ann. Bryol., suppl. vol. 4, pp. 1–231.

1950. The future of exotic cryptogamic botany. Bryologist, 53:1–9.

VOTH, PAUL D.

1943. Effects of nutrient-solution concentration on the growth of *Marchantia polymorpha.* Bot. Gaz., 104:591–601.

WALDHEIM, STIG

1947. Kleinmoosgesellschaften und Bodenverhältnisse in Schonen. Bot. Not., suppl. vol. 1, pt. 1, pp. 1–203.

WALLACE, ALFRED RUSSEL

1908. Notes of a Botanist on the Amazon and Andes by Richard Spruce, Ph.D. 2 vols. London: Macmillan and Co.

WALSH, H.

1947. Geotropism and phototropism in the sporophyte of *Splachnum sphaericum* Linn. fil. Naturalist, 1947:137–139.

WALTON, J.

1928. Carboniferous Bryophyta. II. Hepaticae and Musci. Ann. Bot., 42:707–716.

WARNSTORF, CARL

1911. Sphagnales-Sphagnaceae (Sphagnologia Universalis). *In* Engler's Das Pflanzenreich. iv + 546 pp. Leipzig: W. Engelmann.

1912–1913. Zur Bryo-geographie des Russischen Reiches. Hedwigia. Vols. 53, 54. (Also issued as repaged separate publication, 300 pp.)

1916. Pottia-Studien als Vorarbeiten zu einer Monographie des Genus "Pottia" Ehrh. sens. str. Hedwigia, 58:35–152.

WATSON, H.

1947. Woodland Mosses. 48 pp. Forestry Commission Booklet. London: H.M.S. Stationery Office.

WATTS, W. WALTER, and THOMAS WHITELEGGE

1902–1905. Census Muscorum australiensium. A classified catalogue of the frondose mosses of Australia and Tasmania, collated from available publications and herbaria records. Proc. Linn. Soc. New South Wales. Suppl. to Vols, 27, 30.

WETTSTEIN, F. VON

1942. Ueber einige Beobachtungen und experimentale Befunde bei Laubmoosen. Ber. Deutsch. Bot. Ges., 60:394–414.

WETTSTEIN, F. VON, and J. STRAUB

1942. Experimentale Untersuchungen zum Artbildungsproblem. III. Weitere Beobachtungen an polyploiden Bryum-Sippen. Zeitschr. f. induktive Abstammungs- u. Vererbungslehre, 80:271–280.

WILLIAMS, ROBERT STATHAM

1921. Mosses. Rept. Canadian Arctic Expedition, 1913–18, Bot., 4(pt. E):1–15.

WOLCOTT, GORDON B.

1941. The effect of colchicine on a hepatic. Journ. Hered., 32:66–70.

WORONOFF, G.

1930. Nouvelles contributions à la flore bryologique de la Caucasie. Rev. Bryol., n.s., 3:105–122.

WYNNE, FRANCES E.

1944a. Studies in Drepanocladus. II. Phytogeography. Amer. Midl. Nat., 32:643–668.

1944b. Studies in Drepanocladus. IV. Taxonomy. Bryologist, 47:147–189.

1945. Studies in Calliergon and related genera. Bryologist, 48:131–155.

ZODDA, J.

1934. Flora Italica Cryptogama. Pars IV: Bryophyta. Hepaticae. 300 pp. Rocca S. Casciano: L. Cappelli.

PTERIDOLOGY

By IRENE MANTON
University of Leeds

THE PTERIDOPHYTA are a central group in the botanical system and their study impinges at once on some of the most fundamental problems of morphology and evolution which have yet been formulated. The interpretation of the situation within the group is profoundly affected by available knowledge of plants of other types (gymnosperms, flowering plants, bryophytes, and algae) and they contribute at least as much to students of other groups as they draw from them. As the oldest known vascular plants on the earth's surface, the fossil Pteridophyta are indeed of unique importance to the whole of botany and more than in any other group, except perhaps the gymnosperms, the study of fossils has become inseparable from that of the living representatives and colors much of our attitude towards them.

In the pre-Darwinian period (n.b., *Origin of Species,* 1859) at the beginning of our "century" this was naturally not apparent. It is true that a beginning had been made by the pioneer researches of Brongniart (1828–1838) and Goeppert (1841), but effective correlation of fossils with living plants was scarcely possible on the basis of knowledge then available, as is clearly brought out in a work such as that of Lindley and Hutton (1831–1837) in which Brongniart's coal-measure Lycopods (*Lepidodendron, Sigillaria,* etc.) are discussed as possible dicotyledonous trees. There was indeed considerable uncertainty, in spite of excellent work by great morphologists such as von Mohl, about the fundamental characters for taxonomic separation of even major groups of land plants. This is clearly displayed in standard publications of the textbook type of which Lindley's much-used *Vegetable Kingdom* is a fair sample. In this (3d ed., 1853) we find *Equisetum* grouped with the liverworts and before the mosses, Lycopodiales is divided into Lycopodiaceae and Marsiliaceae, and Filicales consist of three families, Ophioglossaceae, Polypodiaceae, and Davalliaceae. A confusion of this kind can obviously be reduced to order only by a more detailed and accurate knowledge than was available at the time, of life histories, structure (internal as well as external), development, and fossil history, all interpreted with the idea of evolution in mind. In the course of a century much progress has been made in all these lines until one may think that, short of the discovery of wholly new fossil groups, our modern classification into the major subdivisions of Psilophytales, Psilotales, Sphenophyllales, Equisetales, Lycopodiales, and Filicales (cf. Bower, 1935) is perhaps a true and permanent one. Even this is, however, still subject to change of nomenclature (cf., for example, fig. 2), and when one realizes that the definitive separation of the Psilotales from the Lycopodiales, no less than the discovery of the Psilophytales, is effectually the work of the twentieth century (although with pioneer literature further back), one must expect that our present scheme, though undoubtedly truer than that of a century ago, may still perhaps not be final.

Modern work on the Pteridophyta may be considered to begin with the publication in 1851 of Hofmeister's *Vergleichende Untersuchungen.* This book, better known to some readers as *The Higher Cryptogamia* in the later English edition of 1862, is a landmark in the history of botany and probably the most important botanical product of either year. It is the first, and still in many ways the most detailed and informative, general account of the life histories and reproductive structures of the main types of Bryophyta and Pteridophyta together with some, though less complete, reference to the gymnosperms. Within the Pteridophyta there are descriptions of prothalli, sex organs, and developmental stages in numerous ferns, including *Pilularia, Marsilea, Salvinia, Botrychium,* and *Ophioglossum* (though this only at second hand, quoting Mettenius) as well as *Equisetum, Selaginella,* and *Isoetes.* At one stroke the facts of alternation of generations are spread before one almost in their entirety, and indeed we only need to quote the subsequent addition of the nuclear cycle to the story (Strasburger, 1894) and the discovery of apogamy (Farlow, 1874; De Bary, 1878) and apospory (Druery and Bower, 1884; Bower, 1887) to have substantially our present knowledge of the basic facts of the pteridophytic life cycle. Induced apogamy as a facultative process resulting from prevention of fertilization in a normal sexual species was detected by Heim (1896) and further elucidated by Lang in 1898. Induced apospory, as opposed to the genetically determined sort, was produced on detached fern leaves by Goebel (1908) and, by another method on young leaves *in situ,* by Lang (1924). To these observations and experiments the cytological facts, and in particular those of the polyploid series, have subsequently been added (cf. Lawton, 1932; Manton, 1932; Döpp, 1932; Duncan, 1941; and Manton, 1950). Morphological and experimental observations have been extended to other species (for further literature see Campbell, 1918, and Verdoorn, 1938) and a recent renewed interest in fern prothalli is contributing gametophytic characters to discussions of phyletic details (cf. Stokey, 1951). In a first reading of Hofmeister, however, the absence of these later developments is unimportant. It requires an effort of mind to realize that the date of the *Vergleichende Untersuchungen* is pre-Darwinian and that the logical coherence which it introduces into the taxonomy of the major groups of land plants is not a result of evolutionary thinking but is one of the most spectacular achievements of the comparative morphological study of development.

Speculative thinking 'round the facts of alternation of generations followed later and need not be discussed in detail here since much of it will doubtless have been recorded in connection with other groups of plants, such as the Bryophyta, to which it is equally relevant. An excellent short summary of the period starting with Čelakovský (1874) to the publication of *The Origin of a Land Flora* by Bower in 1908 is given by Bower (1935, pp. 484–491). Both these last publications are important for the clear exposition of the view that "the Archegoniate sporophyte, or diplophase, is a stage interpolated in the course of evolution between the successive events of syngamy and meiosis; and that the neutral somatic development is not strictly homogenetic with the sexual. . . ." (Bower, 1935, p. 491.) This idea of the gradual interpolation of a new phase into a previously simpler sexual life history, as an essential part of the transmigration to the land, illustrates, among other things, the radical change in general outlook which the idea of evolution introduced into the interpretation of Hofmeister's facts. It also gives an indication of the nature of one of the stimuli towards intensive fact-gathering which characterized the late nineteenth and early twentieth century.

One of the greatest lacunae in *The Higher Cryptogamia* itself is due to the fact that certain groups eluded description. In particular the homosporous lycopods and other genera with subterranean prothalli took nearly the whole following century to elucidate and in some respects our knowledge is still incomplete. The reason is that their spores do not germinate readily, if at all, in cultivation and prothalli in nature are infrequent and difficult to find. A history of their discovery is summarized in the introduction to Bruchmann (1898). Spores of *Lycopodium indundatum* had been induced to germinate by De Bary in 1858 but they only developed through a few cell divisions and adult prothalli attached to young plants were only found in this species for the first time by Goebel (1887). In the meantime Fankhauser (1873) had found young plants of *L. clavatum* attached to prothalli and one of these is illustrated in the second English edition of Sachs's textbook (1882). A fuller account of the European species is, however, the work of Bruchmann himself. His classic volume of 1898 contains descriptions, beautifully illustrated with pencil drawings, of gametophytes and numerous developmental stages for *L. clavatum, L. annotinum, L. complanatum, L. selago* and *L. inundatum* (i.e., all the European species). An extension to the tropics with, in particular, the description of the important prothallial types found in *L. cernuum* and *L. phlegmaria,* was carried out in Java by Treub (1884–1889). The relevance of these for an understanding of lycopods in general was pointed out by Lang (1899) in a paper describing prothalli and young plants of *L. clavatum* discovered in Scotland and was discussed again, and very helpfully, by Holloway in a series of papers (1915–1920) describing comparable stages for species of *Lycopodium* in New Zealand. Spore germination leading to mature prothalli was first achieved by Bruchmann in 1910 and this paper is still the most authoritative work on the subject.

With regard to other saprophytic types there is a very beautifully illustrated account of *Ophioglossum vulgatum* by Bruchmann in 1904 and some other observations can be obtained from Campbell (1911, 1918) and Manton (1950). *Helminthostachys,* the last remaining genus of Ophioglossaceae was described by Lang in 1902.

The most difficult to elucidate of all the saprophytic gametophytes have proved to be those of the Psilotales. Prothalli were not found for either *Psilotum* or *Tmesipteris* until the twentieth century and in both cases our knowledge rests principally on the work of Holloway in New Zealand. A brief history will be found in Holloway (1939). It begins in 1917 with a description of adult gametophytes and some young plants of *Tmesipteris* in Australia by Lawson. A fuller account of prothalli and young embryos of *Tmesipteris* in New Zealand came from Holloway himself in 1918 and descriptions of the embryo and sporeling followed in 1921. One of the more important conclusions, which is clearly expressed even in the 1918 paper, is to emphasize the primitive nature of the rootless habit of *Tmesipteris* and the apparently primitive character of its embryology. The desirability of separating the Psilotales from the Lycopodiales is stressed, and this point of view, though not in itself original to Holloway, has received its strongest support, apart from the fossil evidence, from his work, and is now generally accepted. Knowledge of *Psilotum* prothalli also dates from 1917 with preliminary descriptions of certain stages independently by Darnell Smith and Lawson. A fuller description comes from Holloway in 1939 (preliminary note in 1938). This paper, while confirming the close resemblance of *Psilotum* to *Tmesipteris* in matters of embryology and in particular in showing the all-important character of the young plant as consisting of a dichotomously branching cylindrical axis with apical growth and central vascular tissue but without roots or appendages in the early stages other than superficial hairs, adds one other fact of unique interest. The apical growth, dichotomous branching, and cylindrical form of the subterranean prothalli, while agreeing with *Tmesipteris,* also recall small pieces of rhizome, and this resemblance is increased by the discovery that, in all really large prothalli, traces of central vascular tissue were also present.

This last observation is the reason why it has seemed important to trace in such detail the growth of knowledge of life histories in the more difficult pteridophyte groups. The interpretation of the observation was left by Holloway himself, with becoming caution, as *sub judice.* One suggestion was that the large vascular prothalli were abnormal, and this possibility is a real one since it was later shown (Manton, 1942) that all of Holloway's prothalli, both vascular and nonvascular, were cytologically diploid and derived from tetraploid sporophytes. Haploid prothalli have not yet been found and, until they are, the risk of abnormality cannot be dismissed. There is, however, no precedent for the supposition that teratological structures are necessarily caused by polyploidy as such and an alternative possibility must also be kept in mind. This is that we may have here not an abnormal, but a vestigial, structure of a very primitive kind. We are indeed being confronted with an alternative view of alternation of generations in the land plants which is diametrically opposed to that expressed by Bower in *The Origin of a Land Flora* (1908) and which recalls very strongly that expressed by Lignier in 1903. The latter postulated an ancestor for all the archegoniates, his "prohepatica," in which both generations were similar except for their reproductive structures and composed of simple dichotomous thalli with apical growth, nonvascular in the ancestor of the bryophytes and perhaps vascular at a later stage in the ancestor of the pteridophytes. This suggestion is obviously of the closest relevance to the facts of life history in the Psilotales as they are at present known. More evidence is needed both from living plants and more especially from fossils before further progress can be made. But in contrasting the views of Lignier and Bower, both of whom have contributed in an essential way to botanical thought, we can epitomize much of the constructive thinking which has been given to the subject of alternation of generations in the Pteridophyta in the century which has succeeded Hofmeister.

One of the more obvious effects of Hofmeister's work was to remove permanently the obscurity about diagnostic criteria for delimiting the main groups of archegoniates, and we may quote in illustration of this another early English textbook, that of Berkeley (1857). In this we find under the heading Filicales, which corresponds to our use of the word Pteridophyta, the following list:

FILICALES
1. Filices
2. Ophioglossaceae
3. Equisetaceae
4. Marsiliaceae
5. Lycopodiaceae under which are included *Lycopodium*, *Selaginella*, *Isoetes*, *Phylloglossum*, *Psilotum*.

There is little morphology and no anatomy in Berkeley but the progress made in these can be traced in the various editions of Sachs's great *Textbook*, which first appeared in German in 1868 and subsequently passed through numerous editions, enlargements, and translations, dominating botanical teaching for at least thirty years. Sachs's *Textbook* was the prelude, and doubtless also the stimulus, to a great development in morphological botany which took place at the end of the nineteenth century. At first this was dominated by the great German morphologists, notably Goebel and De Bary. Goebel's *Grundzüge der Systematik* was published in 1882 (Eng. trans., 1887, under the title, *Outlines of Classification and Special Morphology*) as part of a fundamentally revised fourth edition of Sachs. This was followed in 1897 by the first edition of the *Organographie*, a work which subsequently passed through three editions during its author's lifetime (3d ed. 1930), embodying and summarizing an enormous amount of personal observation on the biological activity of Pteridophyta and Bryophyta regarded as living organisms rather than as units in a taxonomic system. Goebel also developed the experimental approach (1908), the subsequent history of which, accumulated over the century, will be found in Verdoorn (Williams, 1938) and more recently in Wetmore and Wardlaw (1951).

In addition to his work in experimental morphology, Goebel's interest in development led him, at an early date (1880, 1881) to an intensive study of the development of pteridophyte sporangia in representatives of most of the main groups, with the object of tracing in detail the origin of the sporogenous tissue. In the course of this he introduced a number of new concepts which are still retained in now familiar words, such as "archesporium." The division of the Pteridophyta into "eusporangiate" and "leptosporangiate" types also dates from this time, his grouping being as follows:

I. LEPTOSPORANGIATES
- A. Filices
  - 1. Homosporous (Polypodiaceae, Gleicheniaceae, Cyatheaceae, etc.)
  - 2. Heterosporous (Salviniaceae)
- B. Marsiliaceae

II. EUSPORANGIATES
- A. Filices
  - 1. Marattiaceae
  - 2. Ophioglossaceae
- B. Equisetales
  - 1. Calamites
  - 2. Equisetaceae
- C. Sphenophyllales
- DD. Lycopodiales
  - 1. Lycopodiaceae—homosporous (*Lycopodium*) heterosporous (*Lepidodendron*, etc.)
  - 2. Psilotaceae
  - 3. Selaginellaceae
  - 4. Isoetaceae
- E. Gymnospermae
- F. Angiospermae

This scheme is of the greatest possible interest since Goebel, though not primarily a taxonomist, is one of the earliest professed evolutionists to consider taxonomic problems in their broader aspects; he is also one of the very first to include the fossil groups as part of a scheme involving living plants. In England the first inclusion of fossils in a botanical text is in the notes added by Vines to the second English edition of Sachs's *Textbook* published in 1882. When we realize further that certain groups, such as the Sphenophyllales, were still very imperfectly known (first observations on anatomy, Renault and Zeiller, 1870–1873; Williamson, 1874) and that as late as 1881–1886 *Sphenophyllum* was interpreted by Renault himself as a member of the Rhizocarpeae related to *Salvinia*, the modern tone of Goebel's scheme is very impressive. It is also of interest to notice that by including the gymnosperms and angiosperms in one coherent scheme with the Pteridophyta, Goebel is in fact expressing phyletic views about their origin which, in the text of his paper, he discusses somewhat more explicitly. The leptosporangiate ferns he regards as so different from seed plants as to be in no sense ancestral to them, and the correlation between an indusium and an integument or between the sporangium and a nucellus can therefore be an analogy only; a highly instructive comment on current usage since Hofmeister. Goebel's views on the origin of seed plants are also interesting. He derives the conifers from the lycopods and the cycads from Marattiaceae, both Eusporangiate groups. These views are no longer held by any botanist, but it is doubtful whether anything better could have been suggested on the evidence available in 1881.

In 1881, the most conspicuous void in knowledge regarding the pteridophytes was that of vascular anatomy. It is true that in 1877 De Bary's *Vergleichende Anatomie der Vegetationsorgane der Gefässflanzen* had appeared belatedly as the last volume in a comprehensive textbook originally planned in 1861 to cover the whole of botany under the editorship of Hofmeister, a project which had been much impeded by the successive deaths of all the original contributors except Sachs and De Bary. This book, however, is of greater intrinsic significance in the history of flowering-plant anatomy than it is for the vascular cryptogams. Interest in plant anatomy in general was undoubtedly stimulated by it and it is still a valuable source of reference for teaching purposes. But for the Pteridophyta it may be suspected that its greatest effect may have been indirect, by focusing the attention of the young F. O. Bower on the need for further exploration of the vascular structure of this group in the course of translating the text. This translation, in collaboration with D. H. Scott, for the English edition of 1884, appeared under the title, *Comparative Anatomy of the Phanerogams and Ferns.*

Almost concurrently with this we have the publication of van Tieghem's *Traité de Botanique*, 1884 (2d ed., 1891). This great French textbook has never received the publicity accorded to the German textbooks of Sachs and later of Strasburger (1894) but it stimulated and expressed the work of an important school of French plant anatomists. To van Tieghem himself we owe the introduction of the concept of the stele (van Tieghem and Douliot, 1886), without which the descriptive exploration of the Pteridophyta is impossible. The application of this concept to the Pteridophyta was in part explored by van Tieghem's own school (cf., for example, the *Traité,* 2d ed., 1891; van Tieghem, 1888, etc.) and then the work spread to England, America, and Holland.

An excellent historical survey of the contribution made by van Tieghem and his immediate successors was published in 1902 by Schoute in a book which also did much to standardize our present terminology by, among other things, sweeping away one of van Tieghem's less felicitous concepts, namely, the attribution of polystely to the ferns. Schoute's bibliography is instructive. It includes Jeffrey (1897) for the invention of the words "protostele" and "siphonostele," Gwynne-Vaughan (1897) for the introduction of the word "meristele"; Gwynne-Vaughan again in 1901 for the word "solenostele" and Brebner (1902) for the word "dictyostele." Brebner's paper contains an extensive and interesting glossary of contemporary anatomical terms, many of which are still in use, and Jeffrey's paper is of special interest for the clear statement (Jeffrey, 1897, p. 869; elaborated later in Jeffrey, 1903):

> In the Filicales the siphonostelic modifications arose in connection with the support of large leaves, and hence is called phyllosiphonic. In the Lycopodiales, and probably the Equisetales, it is related to the support of branches and hence may be termed cladosiphonic.

The implications inherent in this point of view became more generally recognized twenty years later.

The work of the British school of plant anatomists headed by F. O. Bower has been so excellently summarized by the numerous publications of that author (Bower, 1908, 1923, 1926, 1928, 1935) that it need not be discussed in detail. For an independent summary of the position at the time of the publication of the *Land Flora,* reference may be made to Tansley (1908), and for the position twenty years later there is Schoute (1938).

Concurrently with the advance in knowledge of the anatomy of living members of the group, the anatomical study of fossils has been a development of the first importance. A pioneer in this field was Williamson (1871–1883), with Renault in France as an almost exact contemporary. At a later date Williamson collaborated with D. H. Scott (1894–1895) after which Scott carried on alone (1897 *et seq.*). To these authors we owe the first clear outlines of the anatomical structure of the main pteridophyte constituents of the coal-measure flora, together with those which we now know to have been seed plants but which at that time were thought to be fern-allies of the group Cycadofilices.

The effect of this work on the taxonomic system is at once displayed in Engler and Prantl, *Die natürlichen Pflanzenfamilien,* of which the first parts of the volume on Pteridophyta appeared in 1898. This contains a supplement on the fossils of Potonié and the main groups recognized (both living and fossil) are as follows:

Class I. Filicales
1. Leptosporangiatae (10 families of ferns including Marsileaceae and Salviniaceae)
2. Marattiales
3. Ophioglossales

SUPPLEMENT ON SUPPOSED FOSSIL FERN LEAVES

Class II. Sphenophyllales

Class III. Equisetales
1. Equisetaceae
2. Calamariaceae

Class IV. Lycopodiales

1. Eligulatae
   - Lycopodiaceae
   - Psilotaceae

2. Ligulatae
   - Selaginellaceae
   - Lepidodendraceae
   - Bothrodendraceae
   - Sigilariaceae
   - Pleuromeiaceae
   - Isoetaceae

SUPPLEMENT ON CYCADOFILICES

With the turn of the century, in addition to those continued trends of work on the various topics which have already been traced, by far the most important contributions to understanding of the Pteridophyta have come from the further discoveries in fossil botany. Interest in this was very greatly increased by several publications which appeared at this time and were intended for the general botanical reader rather than a geologist or specialist. Renault's *Cours de Botanique Fossile* (1881–1886) was one of the earliest, closely followed by Solms-Laubach's *Einleitung in die Paläophytologie von botanischen Standpunkt aus* (1887; Eng. trans., 1891). Then in 1899 we have the first volume of Seward's *Fossil Plants,* and in 1900 Zeiller's *Éléments de Paléobotanique* and the first edition of Scott's *Studies in Fossil Botany.*

Comparison of the contents of the three editions of Scott's *Studies* (1st ed., 1900, 2d ed., 1908, 3d ed., 1920) will show the nature of the developments in fossil botany in the first quarter of the twentieth century. More recent information will be found in Hirmer (1927), Darrah (1939), Walton (1940), Halle (1940), Emberger (1944), Arnold (1947), and doubtless elsewhere.

One of the most important events of the early twentieth century was the discovery by Oliver (see Oliver and Scott, 1905) of evidence for the seed of *Lyginodendron.* This was rapidly followed by Kidston's account of fertile structures of *Neuropteris* and further publications by Scott and Oliver, which are summarized in detail in the second edition of Scott's *Studies* (1908). These discoveries remove the Cycadofilices out of the Pteridophyta and into the gymnosperms, where they still are under the general name of pteridosperms. A full account of the establishment and subsequent fate of the pteridosperms will doubtless have been included in the paper on gymnosperms and need not be repeated here. They are, however, of importance to the present group because they are the cause of a popular fallacy which has proved very hard to dispel and which, unconsciously, is still liable to affect botanical thought and teaching, the fallacy, namely, that the coal-measure period was an age of ferns. We now know that the true ferns were only present in the coal measures in small and archaic forms (the Coenopteridales) very unlike living ferns and that probably all the conspicuous fernlike leaves of that era belonged to seed plants.

Of greater importance even than the removal of the pteridosperms was the advent of the Psilophytales. The first two of these primitive land plants had been discovered and named by Dawson at a very early date (1859 for *Psilophyton* and 1871 for *Arthrostigma*) in Middle and Lower Devonian rocks from the Gaspé Peninsula in eastern Canada, but, though known to geologists and to some botanists, they were too unfamiliar in type to be assimilated into the system for nearly fifty years. Attention was, however, arrested, even during the first World War, by the almost simultaneous discovery of both *Psilophyton* and *Arthrostigma,* along with fragments of other plants, notably the putative bryophyte sporogonites, in Lower Devonian rocks of Röragen in Norway (Halle, 1916) and by the report of the wonderfully preserved Rhynie fossils from Scotland (Kidston and Lang, 1917 *et seq.*).

The successful study of the plants of the Lower Devonian and other early floras is probably the most important contribution which the Pteridophyta have made to botanical thought since Hofmeister. Some highly instructive comments on it may be quoted verbatim from Halle's 1916 paper. Under the heading "General Botanical Conclusions" he says (p. 35):

The botanical interest presented by the oldest known land-floras, of which the Röragen flora is one of the most typical representatives, is naturally connected with the question of the relative antiquity of the different phyla of land-plants. The Pteridophyta stand naturally in the foreground; and in regard to these the interest centres round the problem whether the microphyllous or the megaphyllous forms, the Lycopsida or the Pteropsida, are the more primitive. This is a question on which information may well be expected to be gained from the fossils, provided the record goes sufficiently far back. It is the general opinion that the Devonian floras are already too far advanced to throw any light on this question. In the well developed floras of Kiltorkan, Bear Island, etc., to which attention has usually been confined, both megaphyllous forms such as *Archaeopteris* and microphyllous forms such as *Cyclostigma*, occur as dominant elements. These floras, however, belong to the Upper Devonian. The Lower Devonian floras, from reasons mentioned in the Introduction, have mostly been neglected, although it would appear that a critical review of the available material would lead to the recognition of some noteworthy facts. In the following pages the evidence for the occurrence of respectively the Lycopsida, Pteropsida and the Bryophyta are shortly discussed.

We cannot unfortunately follow the whole discussion here. The essential facts indicating the presence of microphyllous forms, and the apparent absence of any fernlike or megaphyllous forms both from Röragen and from Gaspé, are reviewed and then the author goes on to say:

It might perhaps be suggested, although this is pure speculation, that megaphyllous forms may be evolved from a type like *Psilophyton Goldschmidtii.* The lateral branches of this form already appear to have a bilateral or dorsiventral symmetry. The rapid tapering of the segments of isolated branch-systems similar to the lateral branches of *Psilophyton Goldschmidtii,* suggests a limited growth in some cases. Such lateral branches of limited growth may be imagined to develop laminae by a process of cladodification. A similar development has been suggested by the late Professor Lignier (1903, 1908–11) in his interesting speculations on the first evolution of the different branches of the pteridophytic stock. Lignier even used *Psilophyton princeps* as a starting point. He adopts the view of a diphyletic origin of the leaves of the Pteridophyta, starting from a "prohepatic type" derived from algae. The leaves of the Lycopodiales are distinguished as "phylloids" and regarded as developed phylogenetically by "enation" in the manner of emergences. The frond of the megaphyllous forms, on the other hand, are true leaves formed by differentiation of thallus branches in accordance with current opinion. It would seem that what little is known at present about the Lower Devonian flora is well in accord with Lignier's views. We have in *Psilophyton princeps,* imperfectly though it is known, a plant which has actually existed and which answers well to the type theoretically required as a starting point. Similar plants, with well developed stems and small lateral appendages which may be compared either to emergences or leaves, were dominant in the Lower Devonian flora; and there is reason to regard them as primitive. The geological record available at present indicates that they existed before the fern-type with large fronds, as exemplified by the Upper Devonian *Archaeopteris.* On the other side there is *Psilophyton Goldschmidtii,* which is probably closely related to *Psilophyton* *princeps*, and this form, as set forth above, would seem to furnish us with an intermediate stage required by Lignier's hypothesis. From this point of view the whole pteriodophytic stock would be monophyletic, the Lycopsida and Pteropsida being derived from a common form already vascular. It would thus not be necessary to assume parallel evolution of a similar vascular system along two different lines. The leaves, on the other hand, would be morphologically diphyletic. If the microphyllous habit is regarded as primitive, it would not be necessary to derive the large fronds of the Filicales from the leaves of the Lycopsida through a process of progressive development. In the Filicales, only the paleae or other emergences on the rachis would be homologous with the leaves of the Lycopsida. Such emergences, in the shape of hairs or spines, are strikingly common in Palaeozoic fronds: . . . Finally attention may be called to the coincidence that the circinnate vernation of the fern fronds is paralleled in the branches of *Psilophyton princeps*.

These quotations have been given at length because they convey very clearly the gist of one of the main conclusions which these plants have brought permanently into botany, namely, the conclusion concerning the fundamental difference and relative order of origin of microphyllous and megaphyllous forms. It is possible that the speculations quoted might have been slightly different in detail had they been based on *Rhynia* rather than on *Psilophyton*. Thus one may suspect that less stress might have been laid on the idea of "enation" as opposed to the suggestion, actually made by Tansley (1908) and considered by Lignier (1911), that microphylls in origin are small lateral branches (i.e., small "cauloids" and not enations) as opposed to the large branch systems of megaphylls. Even if this possibility is left open, however, the essential contribution to thought regarding the nature of megaphylls is unaffected and it ties up so closely with the anatomical considerations already mentioned (cf. Jeffrey, 1897) with regard not only to the ferns but to gymnosperms and angiosperms as well (all of which are megaphyllous though not necessarily monophyletic) that it seems unlikely now to be seriously challenged.

Since Gaspé, Röragen and Rhynie, the knowledge of Middle and Lower Devonian floras, and with them of the Psilophytales, has been greatly extended, at first by the work of Lang on Scottish rocks (1927–1937), and later by an extension to other countries, notably by Kraüsel and Weyland (1923–1935) in Germany, Dorf (1933–1934) in the United States (Wyoming), Stockmanns (1940) in Belgium, Hoeg (1942) in Norway (on rocks from Spitzbergen). An excellent early summary will be found in Hoeg (1937), and a later one in Croft and Lang (1942). Finally an extension to still earlier geological formations, all nevertheless containing vascular plants of the Psilophytalean affinity, has been made by Lang (1937) for the Downtonian of Britain and by Lang and Cookson (1930, 1935) and by Cookson (1935) on the Silurian of Australia, which is specially important for showing that somewhat more complex and larger types than *Rhynia* or *Psilophyton* existed at an even earlier date. We are therefore only in possession of knowledge of the merest fragments of what must have been not only the dominant, but a very varied group, at the dawn of the fossil record of land plants.

The impact of this new knowledge on the taxonomic system is still undoubtedly incomplete. The primitive nature of rootless types has emphasized the importance of the living Psilotaceae. On the other hand, the undoubtedly axial nature of the spore-bearing members has affected so fundamentally the previously prevalent concepts of the nature of "sporophylls" that a complete revolution in thought is required in order to assimilate it. The morphological redescription of the fertile parts of microphyllous genera such as, for example, the cone of *Equisetum* or the synangia of *Psilotum*, in terms of sporangiophores, is fairly easy to envisage even if one does not wish to go to the length of using the terminology of the "telome" as postulated by Zimmermann (1930, 1938). The case of the megaphyllous ferns and seed plants is, however, more complicated, and again it may be helpful to quote Halle. In discussing naked forked axes bearing terminal sporangia known as Dawsonites and thought to be the fertile parts of *Psilophyton* he remarks:

". . . the sporangia of Dawsonites recall those of certain Upper Devonian and Carboniferous ferns generally considered as primitive, as for instance *Dimeripteris*, or perhaps *Stauropteris*, according to Lignier (1908–11). . . . The chief points of resemblance between the fertile fronds of certain Primifilices and *Dawsonites arcuatus* are the large size of the sporangia and their apical position on branches of special fronds or pinnae without developed laminae. Among the fronds of the Lower Carboniferous and Upper Devonian, the common occurrence of "modified" fronds bearing sporangia but no flattened pinnules is very striking. . . . In the Lower Devonian, finally, we find frondlike structures bearing sporangia but no fronds with developed laminae. One can hardly escape the conclusion that the "modified" fertile fronds may represent the primitive state in this case and that the flattened pinnules are a later development as suggested by Professor Lignier. The sporangia would then be pre-existent in respect to the laminae of the pinnules.

This last sentence has a bearing, not only on our view of the nature of primitive ferns, but, by an extension which Halle himself visualized (1937), can also be applied to the seed plants if, as may have been the case, the seed also is older than the lamina of a leaf. The fossil evidence is inconclusive here and it would be out of place to discuss it further. It is, however, necessary to refer to it in passing because it raises the point of view that, although the megaphyllous types at present known contain both ferns and seed plants, the megaphyllous habit which they both share may be homoplastic and the only common ancestor uniting the Filicales and Gymnosperms may in fact be the Psilophytales.

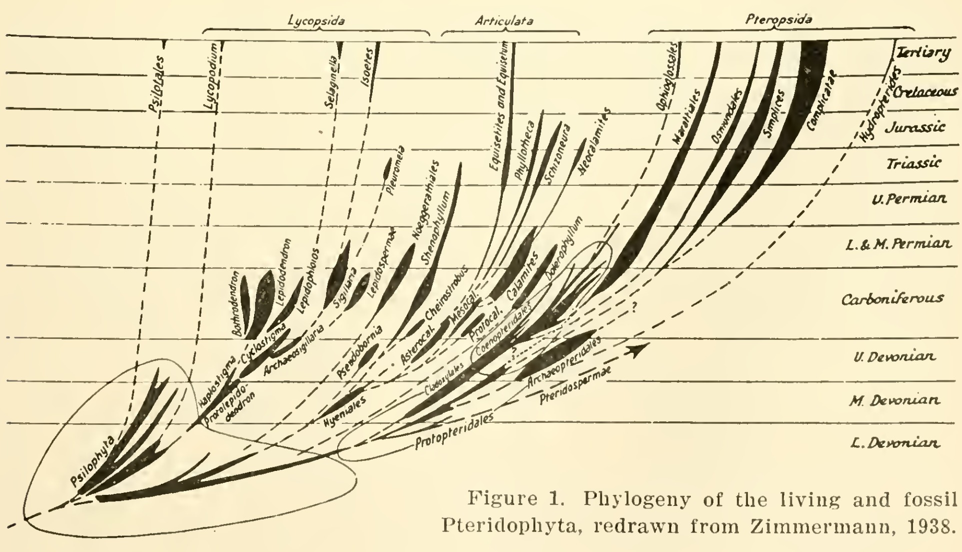


Figure 1. Phylogeny of the living and fossil Pteridophyta, redrawn from Zimmermann, 1938.

A diagram summarizing some of these phyletic views and the facts of distribution in time of the known living and fossil members of the Pteridophyta is reproduced as figure 1 after Zimmermann, 1938. It indicates very clearly what is fact and what is hypothesis and needs no further explanation.

One further topic must now be considered, which may perhaps form somewhat of an anticlimax compared with those just discussed but which must be dealt with last since active work on it is still in progress as the "century" closes. This is the detailed classification within the various surviving groups of Pteridophyta.

The history of knowledge on the various genera and species of Psilotales, Equisetales, and Lycopodiales need not be discussed since most of the relevant facts are summarized conveniently in the several chapters in Verdoorn (1938) devoted to these groups. On the other hand the ferns, by their mere numbers (some 10,000 known species), have necessarily developed a very considerable taxonomic literature of their own. The early history is summarized in Smith (1875) and the later history in Christensen (1938), in the "Introduction" to Copeland (1947) and, from a different point of view, in Bower's *Ferns,* Volume I (1923). At the beginning of our "century" in spite of the existence of important taxonomic works such as those of Schott (1834), Moore (1857), Fée (1850–1852), Presl (1836), the prestige of the elder Hooker was so great that in the middle of the nineteenth century he effectively dominated fern taxonomy in a way which all recent systematists feel to have been disadvantageous. Hooker's system of classification was summarized in Hooker and Baker's *Synopsis Filicum,* published in 1865–1868 after Hooker's death. Now that it has grown by accretion out of its original usefulness as developed in the successive volumes of the Hooker's *Species Filicum* (1844–1864), we now see it to be an unwieldy assemblage of too many species grouped in too few genera, based on too few criteria in an almost Linnean arrangement. The work of turning this into a phylogeny has taken the whole of the century and is still incomplete. As in the larger groups, the first requirement in the consideration of genera and species has been to determine the criteria which are taxonomically effectual and from them to deduce which characters are most primitive and which are advanced. In the effort to do this it has been necessary to disentangle numerous cases of parallel evolution which make individual characters of less value than at first they appeared. This has involved the use of an increasing number of characters both external and internal taken together and progress has naturally, at any one time, been very closely dependent on the state of knowledge of the Pteridophyta as a whole, which has just been outlined. Thus in Engler and Prantl's treatment of the ferns (1898–1902) already quoted (p. 307) the order of citation begins with the Leptosporangiatae followed by Marattiales and Ophioglossaceae while within the Leptosporangiatae the order of citation is as follows:

Hymenophyllaceae	Gleicheniaceae
Cyatheaceae	Schizaeaceae
Polypodiaceae	Osmundaceae
Parkeriaceae	Salviniaceae
Matoniaceae	Marsiliaceae

Diels, the author of most of this part of Engler and Prantl, was an evolutionist and his order of citation, though not strictly a phylogeny, is nevertheless phyletic in general intention. Many details are, however, traditional in the sense that they go back at least to Goebel (1881) and often much earlier. An important new idea had nevertheless been contributed by Campbell in 1890 and immediately accepted by Bower, namely, that the Eusporangiateae and not the Leptosporangiatae represent the most ancient type of ferns. This reverses the order of citation of the three main groups of Filicales in the list quoted on page 307 and it also provides, for the first time, some definite criteria for attempting to recognize the primitive groups within the Leptosporangiatae. The story of how this was done, largely by the work of Bower, is very well known and is described in the first volume of Bower's *Ferns* (1923). The detailed application of Bower's selected criteria for the delimitation of primitive groups is contained in Volume 2 of the *Ferns* (1926). The primitive position there assigned to the Gleicheniaceae, Schizaeaceae, Hymenophyllaceae, and Osmundaceae is now generally accepted (cf. Copeland, 1947) but these still contain only a minority of living leptosporangiate ferns, the greater number of which

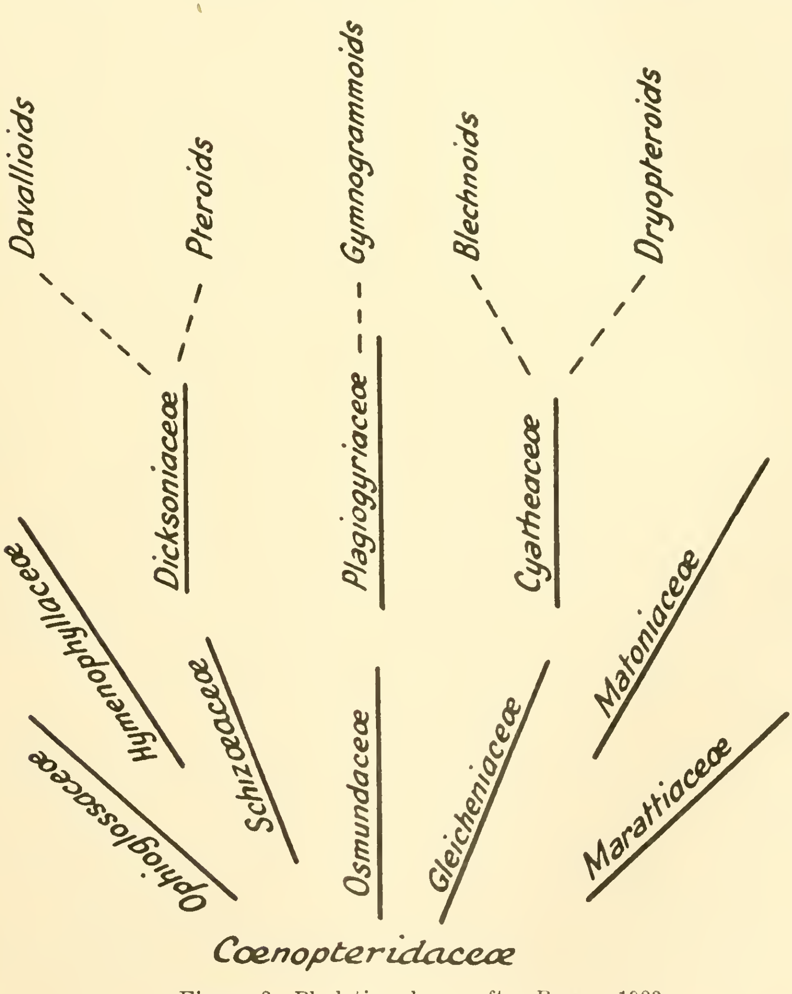


Figure 2. Phyletic scheme after Bower, 1923.

belong to the old composite family "Polypodiaceae," which make up the contents of Volume 3 of the *Ferns* (1928).

It is hardly surprising that Bower's treatment of the ferns in Volume 3 is less satisfactory than are the contents of Volume 2 because the number of species is here so great and the confusion caused by parallel evolution so difficult to disentangle that the full technique and mental equipment of the professional systematist is necessary to deal with them. This, Bower was not, and the most obvious mistakes which can already be recognized as such arise from this cause. For the same reason, it is precisely here that the contribution of professional taxonomists in the twentieth century has been the greatest. Foremost among these has been Carl Christensen. In the *Index Filicum* (1905–1906), the standard compilation to which (with the three supplements published in 1913, 1917 and 1924) all modern problems of nomenclature in the ferns are referred, Christensen followed Diels in general classification, although the individual genera are quoted alphabetically. The growth of Christensen's own views is, however, traceable in various monographs between 1907 and 1932 and these views were summed up in 1938 in the form of a short sketch of a revised classification, which, however, the author did not live to develop further. Some of Christensen's ideas, notably those concerning the subdivision of the vast and heterogeneous genus *Dryopteris* were, however, already being applied, notably by Ching (1935–1938), and many of them emerge again, though with additions, in the two most modern revised taxonomic schemes, published independently and almost simultaneously by Holttum (1946) and Copeland (1947).

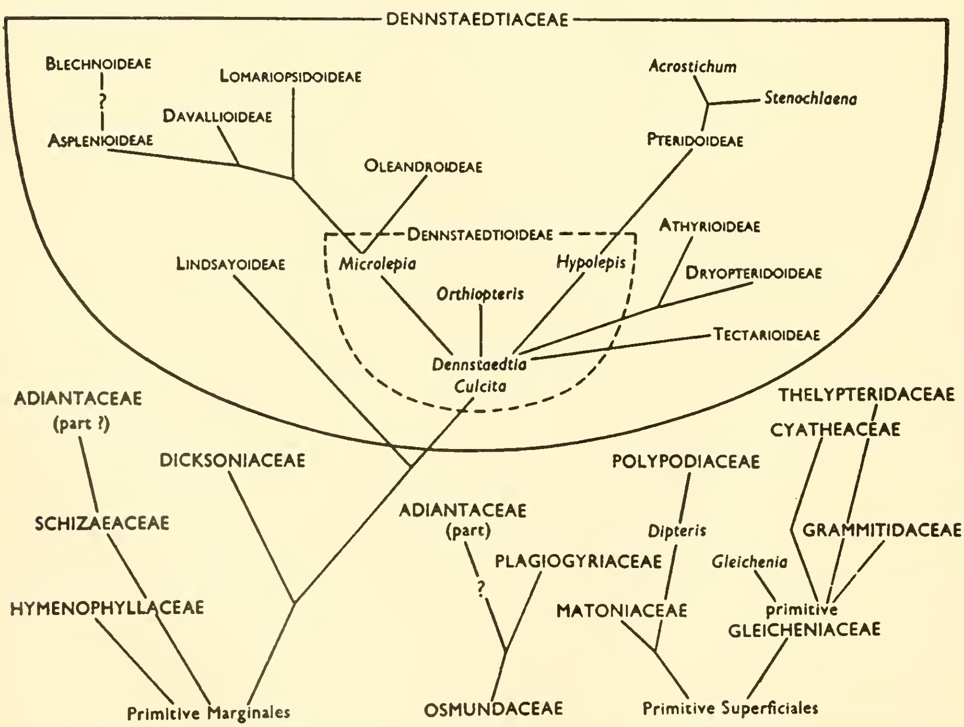


Figure 3. Diagram showing the interrelations of the various groups of ferns according to Holttum, 1949.

A detailed enumeration of the differences between Holttum's scheme and Copeland's was published by Holttum (1949), to which the reader is referred. It is sufficient to say here that, of the two, Holttum's scheme is the more explicitly phyletic, embodying a very great deal of the work outlined on previous pages in his view of the nature of the primitive prototype of the Polypodiaceae. In Holttum's view the genus *Dennstaedtia* conforms most nearly to the hypothetical primitive ancestor of the great majority of "polypodiaceaceous" leptosporangiate ferns, a view which is very clearly expressed in his phyletic diagram reproduced here (fig. 3) from the 1949 paper. It is perhaps of interest to contrast this with Bower's earlier scheme, which is here reproduced as figure 2. That it is an improvement on this scheme in many particulars is already apparent from the evidence of the latest considerable source of new facts, namely that from chromosomes (cf. Manton, 1950), although it is too soon to say how much further modification will be needed before a generally agreed arrangement is reached.

Summing up, we may say that while one of the most active growing points in pteridophyte taxonomy at the close of the century in 1951 concerns the modern ferns, this is only a stage in grafting the idea of evolution onto the Pteridophyta, a process which has taken almost the whole century to effect. During it, whole fields of knowledge, such as life histories, morphology, anatomy, cytology, and paleobotany, have had to be explored for their own sakes but in the process have contributed facts and ideas which are of fundamental importance, not merely for the Pteridophyta but for the whole of botany. The work has been carried out in many countries, of which Germany, France, Britain, America, Holland, Belgium, Norway, Denmark, and Sweden have been quoted in a historical survey which can only touch on headlines without attempting to exhaust the whole immense literature. Since, however, this account has been prepared at the request of the California Academy of Sciences, it may perhaps be of interest to record explicity the more important American contributions. Though relatively few in number these have been of decisive importance on several occasions. It would be invidious to list contemporary writers, but of those of an earlier date we may point to Farlow's discovery of apogamy while on a visit to De Bary's laboratory (1874), the general influence of Campbell's work, more especially regarding the primitive nature of the Eusporangiatae (1890), and the anatomical views of Jeffrey (1897 *et seq.*) as three noteworthy instances. But perhaps most important of all was the discovery of *Psilophyton* by Dawson in Canada in 1859.

LITERATURE CITED

ARNOLD, C. A.

1947. An Introduction to Palaeobotany. New York and London.

BARY, A. DE

1858. Über die Keimung der Lycopodien. Ber. Natürf. Ges. Freiburg. 1858:467–472.

1877. Vergleichende Anatomie der Vegetationsorgane der Gefässpflanzen.

1878. Über apogame Farne und die Erscheinung der Apogamie im Allgemeinen. Bot. Zeit., 36:450–495.

1884. Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns. Eng. trans. Oxford.

BERKELEY, M. J.

1857. Introduction to Cryptogamic Botany. London.

BOWER, F. O.

1887. On apospory and allied phenomena. Trans. Linn. Soc. London Bot., 2(pt. 14): 301–326.

1889. The comparative examination of the meristems of ferns as a phylogenetic study. Ann. Bot., London, 3:305–392.

1908. The Origin of a Land Flora. London.

1923–1928. The Ferns. Vol. 1 (1923); Vol. 2 (1926); Vol. 3 (1928). Cambridge.

1935. Primitive Land Plants. London.

BREBNER, G.

1902. On the anatomy of Danaea and other Marattiaceae. Ann. Bot., London, 16:523.

BRONGNIART, A.

1828–1838. Histoire des végétaux fossiles. Paris.

BRUCHMANN, H.

1898. Über die Prothallien und die Keimpflanzen mehrerer europäischer Lycopodien . . . Gotha.

1904. Über das Prothallium und Keimpflanze von *Ophioglossum vulgatum* L. Bot. Zeit., 62:227–247.

1910. Die Keimung der Sporen und die Entwicklung der Prothallien von *Lycopodium clavatum*, *L. annotinum* und *L. selago*. Flora, 101:220–267.

CAMPBELL, D. H.

1890. On the affinities of the Filicineae. Bot. Gaz., 15:1–7.

1895. The Structure and Development of Mosses and Ferns (Archegoniatae). London. 2d ed., 1905; 3d ed., 1918. New York.

1911. The Eusporangiatea. Carnegie Inst. Publ. No. 140.

ČELAKOVSKY', L.

1874. Bedeutung des Generationswechsels der Pflanzen. Prag.

CHING, R. C.

1935–1938. A revision of the Chinese and Sikkim-Himalayan *Dryopteris* with reference to some species from neighbouring regions, Pts. 1–4. Bull. Fan Inst., Biol. Peking, Vols. 6 and 8.

CHRISTENSEN, C.

1905–1906. Index Filicum. Suppls. I–III (1913, 1917, 1924). Copenhagen.

1907, 1913, 1920. A monograph of the genus *Dryopteris* (American spp.). K. Dansk. Vidensk. Selsk.

1932. The Pteriodophyta of Madagascar. Dansk Bot. Ark., Vol. 7.

1938. *Filicinae*. In Verdoorn, Manual of Pteriodology.

COOKSON, ISABEL C.

1935. On plant-remains from the Silurian of Australia, that extend and connect floras hitherto described. Philos. Trans. Roy. Soc. London, ser. B, 225:127–148.

COPELAND, E. B.

1947. Genera Filicum. Waltham, Mass.

CROFT, W. N., and W. H. LANG

1942. The Lower Devonian flora of the Senni Beds of Monmouthshire and Breconshire. Philos. Trans. Roy. Soc. London, ser. B, 231:131–163.

Darnell-Smith, G. P.

1917. The gametophyte of *Psilotum*. Trans. Roy. Soc. Edinburgh, 52:79.

Darrah, W. C.

1939. Principles of Palaeobotany. Leiden.

Dawson, J. W.

1859. Fossil plants of the Devonian rocks of Canada. Journ. Geol. Soc. London, 15:479.

1871. The fossil plants of the Devonian and Upper Silurian formations of Canada. 2 vols. in 1. Geol. Surv. Canada. Montreal.

Döpp, W.

1932. Die Apogamie bei *Aspidium remotum*. Planta, 17:86–152.

Dorf, E.

1933. A new occurrence of the oldest known terrestrial vegetation, Beartooth Butte, Wyoming. Bot. Gaz., 95:240–257.

1934. Lower Devonian flora from Beartooth Butte, Wyoming. Bull. Geol. Soc. Amer., 45:425–440.

1934. Journ. Geol., 46:377.

Druery, C. T., and F. O. Bower

1884. Observations on a singular mode of development in the Lady Fern (*Athyrium filix-femina*). Journ. Linn. Soc. Bot. London, 21:354–358.

Duncan, R. E.

1941. Apogamy in *Doodia caudata*. Amer. Journ. Bot., 28:921–931.

Emberger, L.

1944. Les plantes fossiles dans leurs rapports avec les végétaux vivants. Paris.

Engler, A., and K. Prantl

1898–1902. Die natürlichen Pflanzenfamilien. Vol. I(4). "Pteridophyta."

Fankhauser, J.

1873. Über den Vorkeim von *Lycopodium*. Bot. Zeit., 1(Jan. 3):1–5.

Farlow, W. G.

1874. Über ungeschlechtliche Erzeugung von Keimpflanzen auf Farnprothallien. Bot. Zeit., No. 12 (Mar. 20), cols. 180–183. Quart. Journ. Micr. Sci., n.s., 14:266.

Fée, A. L. A.

1850–1852. Genera Filicum. Paris.

Goebel, K.

1880–1881. Beiträge zur vergleichenden Entwicklungsgeschichte der Sporangien. Bot. Zeit., 1880:544–551, 560–570; 1881:680–694, 696–704, 713–719.

1882. Grundzüge der Systematik. Leipzig.

1887. Outlines of classification and special morphology of plants. Oxford.

1887. Uber Prothallien und Keimpflanzen von *Lycopodium inundatum*. Bot. Zeit., 1887:160.

1897. Organographia der Pflanzen. 2d ed., 1913: 3d ed., 1930. Jena.

1908. Einleitung in die experimentelle Morphologie der Pflanzen, p. 199. Leipzig. *See also* Organographie (2d ed., 1913), 1:422.

Göeppert, J. H. R.

1841. Die Gattungen der fossilen Pflanzen. Bonn: Henry and Cohen.

Gwynne-Vaughan, D. T.

1897. On polystely in the genus *Primula*. Ann. Bot. London, 11:311.

1901. Observations on the anatomy of ferns. Ann. Bot. London, 15:71.

HALLE, T. G.

1916. Lower Devonian plants from Röragen in Norway. Handl., K. Svensk. Vet.-Akad., 57:1–46.

1937. The position and arrangement of the spore-producing members of the Palaeozoic pteridosperms. Compt. Rend. 2ème Congr. Strat. Carbonifère. Heerlen.

1940. De utdöda växterna. *In* Växternas Liv. Skottsberg, ed. Stockholm.

HEIM, C.

1896. Untersuchungen über Farnprothallien. Flora, 82:329–342.

HIRMER, M.

1927. Handbuch der Paläobotanik. Münich and Berlin.

HOEG, O. A.

1937. The Devonian floras and their bearing upon the origin of vascular plants. Bot. Rev., 3:563–593.

1942. The Downtonian and Devonian flora of Spitzbergen. Skr. Svalb. og Ishavet. Vol. 83. Oslo.

HOFMEISTER, W.

1851. Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen (Moose, Farne, Equisetaceen, Rhizocarpeen, und Lycopodiaceen) und der Samenbildung der Coniferen. Leipzig.

1862. On Development and Fructification of the Higher Cryptogamia and on the Fructification of the Coniferae. London.

HOLLOWAY, J. E.

1915–1920. Studies in the New Zealand species of the genus *Lycopodium*. Pts. I–IV. Trans. New Zealand Inst., Vols. 48–52.

1918. The prothallus and young plant of *Tmesipteris*. Trans. New Zealand Inst., 50:1–44.

1921. Further studies on the prothallus, embryo and young plant of *Tmesipteris*. Trans. New Zealand Inst., 53:386.

1938. The embryo, gametophyte of *Psilotum triquetrum*, preliminary note. Ann. Bot. London, n.s., 2:807.

1939. The gametophyte, embryo, and young rhizome of *Psilotum triquetrum*. Ann. Bot. London, n.s., 3:313–336.

HOLTTUM, R. E.

1946. A revised classification of leptosporangiate ferns. Journ. Linn. Soc. Bot., 53: 123–186.

1949. The classification of ferns. Biol. Rev., 24:267–296.

HOOKER, W. J.

1844–1864. Species Filicum. London.

HOOKER, W. J., and J. G. BAKER

1865–1868. Synopsis Filicum. London.

JEFFREY, E. C.

1897. On the morphology of the central cylinder in vascular plants. Rept. Toronto Meeting Brit. Assoc., p. 869.

1903. The structure and development of the stem in Pteridophyta and Gymnosperms. Phil. Trans. Roy. Soc. London, ser. B, 195:119–146.

KIDSTON, R.

1871. On the fructification of *Neuropteris heterophylla*, Brongniart. Philos. Trans. Roy. Soc. London, ser. B, 197:1–6.

KIDSTON, R., and W. H. LANG

1917–1921. Old Red Sandstone plants showing structure from the Rhynie Chert bed, Aberdeenshire, Pts. I–IV. Trans. Roy. Soc. Edinburgh, Vols. 51–52.

Notes on fossil plants from the Old Red Sandstone of Scotland. I. Hicklingia Edwardi K. and L. Trans. Roy. Soc. Edinburgh, 53:405–407.

KRÄUSEL, R., and H. WEYLAND

1923–1929. Beiträge zur Kenntnis der Devonflora. Pts. I–III. Senckenbergiana. Senckenberg. Naturf. Ges. Abh., 5:40–41.

1933. Die Flora des deutschen Mitteldevons. Palaeontographica, Vol. 78(B).

1935. Neue Pflanzenfunde in rheinischen Unterdevon. Palaeontographica, Vol. 80(B).

LANG, W. H.

1898. Apogamy and the development of sporangia on prothalli. Philos. Trans. Roy. Soc. London, ser. B, 190:187–238.

1899. The prothallus of *Lycopodium clavatum* L., Ann. Bot. London, 13:279–317.

1902. On the prothalli of *Ophioglossum pendulum* and *Helminthostachys zeylanica*. Ann. Bot. London, 16:23–56.

1924. On some deviations from the normal morphology of the shoot in *Osmunda regalis*. Mem. Manchester Lit. and Philos. Soc., 68:53–67.

1925–1932. Contributions to the study of the old red Sandstone flora of Scotland. Pts. I–VIII. Trans. Roy. Soc. Edinburgh, Vols. 15–17.

1931. On the spines, sporangia and spores of *Psilophyton princeps* Dawson, shown in specimens from Gaspé. Philos. Trans. Roy. Soc. London, ser. B, 219:421–442.

1937. On the plant remains from the Downtonian of England and Wales. Philos. Trans. Roy. Soc. London, ser. B, Vol. 227.

LANG, W. H., and ISABEL C. COOKSON

1930. Some fossil plants of early Devonian type from the Walhalla Series, Victoria, Australia. Philos. Trans. Roy. Soc. London, ser. B, 219:133–162.

1935. On a flora, including vascular plants, associated with *Monograptus* in rocks of Silurian age from Victoria, Australia. Philos. Trans. Roy. Soc. London, ser. B, 224:421–449.

LANG, W. H. *See also* R. KIDSTON

LAWSON, A. A.

1917a. The prothallus of *Tmesipteris tennensis*. Trans. Roy. Soc. Edinburgh, 51:785.

1917b. The gametophyte generation of the Psilotaceae. Trans. Roy. Soc. Edinburgh, 52:93.

LAWTON, E.

1932. Regeneration and induced polyploidy in ferns. Amer. Journ. Bot., 19:303–333.

LIGNIER, O.

1903. Equisétales et Sphenophyllales, leur origine filicinéenne commune. Bull. Soc. Linn. Normandie, sér. 5, 7:93–137.

1908. Essai sur l'évolution morphologique du regne végétal. Bull. Soc. Linn. Normandie. (Reprinted 1911.)

1911. Ce qu'il faut entendre par "le meriophte." Bull. Soc. Bot. France, 57:7–8.

LINDLEY, J.

1853. The Vegetable Kingdom. 3rd ed. London.

LINDLEY, J., and W. HUTTON

1831–1837. Fossil Flora of Great Britain. London.

Manton, I.

1932. Contributions to the cytology of apospory in ferns. Journ. Genet., 25:423–430.

1950. Problems of Cytology and Evolution in the Pteridophyta. Cambridge.

Moore, T.

1857. Index Filicum. London.

Oliver, F. W., and D. H. Scott

1905. On the structure of the palaeozoic seed, *Lagenostoma Lomaxi*, with a statement of the evidence upon which it is referred to *Lyginodendron*. Philos. Trans. Roy. Soc. London, ser. B, Vol. 197.

Presl, C. B.

1836. Tentamen Pteridographiae. Prague.

Renault, B.

1870. *See* Renault and Zeiller, 1873.

1881–1885. Cours de botanique fossile. Paris.

Renault, B., and R. Zeiller

1873. Recherches sur l'organisation des *Sphenophyllum* et des *Annularia*. Ann. Sci. Nat., sér. 5, 18:5 *et seq.*

Sachs, J.

1868. Lehrbuch der Botanik (2nd ed., 1882.) Leipzig.

Schott, H.

1834. Genera Filicum. Vindobonae.

Schoute, J. C.

1902. Die Stelär-Theorie. Groningen.

1938. Chapters on "Anatomy" and "Morphology" in Verdoorn, Manual of Pteridology.

Scott, D. H.

1897–1899. On the structure and affinities of fossil plants from the Palaeozoic rocks. Pts. 1–3. Philos. Trans. Roy. Soc. London, ser. B, Vols. 189–191.

1900. Studies in fossil botany. 2nd ed., 1908; 3rd ed., 1920. London.

Seward, A. C.

1899–1919. Fossil Plants. 4 vols. Cambridge.

Smith, J. E.

1875. History of Ferns. London.

Solms-Laubach, H.

1887. Einleitung in die Paläophytologie von botanischen Standpunkt aus. Leipzig.

1891. Introduction to Fossil Botany. Oxford.

Stockmanns, F.

1940. Végétaux Eodevonien de la Belgique. Mém. Mus. Hist. Nat. Belg., No. 93.

Stokey, A.

1951. Contributions by the gametophyte to classification of the homosporous ferns. Phytomorph., 1:39–58.

Strasburger, E.

1884. The periodic reduction in the number of chromosomes in the life history of living organisms. Ann. Bot. London, 8:281–316.

STRASBURGER, E., and F. NOLL, H. SCHENCK, and R. F. W. SCHIMPER
1894. Lehrbuch der Botanik für Hochschulen. Jena.

TANSLEY, A. G.
1908. Lectures on the Evolution of the Filicinean Vascular Tissue. New Phytol. Reprint No. 21. Cambridge.

TIEGHEM, P. VAN
1884. Traité de botanique. (2nd ed., 1891.) Paris.
1888. Recherches comparatives sur l'origine des membres endogènes dans les plantes vasculaires. 9:1–656.

TIEGHEM, P. VAN, and H. DOULIOT
1886. Sur la polystélie. Ann. Sci. Nat., sér. 7, 3:275–322.

TREUB, M.
1884–1890. Études sur les Lycopodiacées. Ann. Jard. Bot. Buitenzenborg, Vols. 4, 5, 7.

VERDOORN, F.
1938. Manual of Pteridology. The Hague.

WALTON, J.
1940. An Introduction to the Study of Fossil Plants. London.

WETMORE, R. H., and C. W. WARDLAW
1951. Experimental morphogenesis in vascular plants. Ann. Rev. Pl., Physiol., 2:269.

WILLIAMS, S.
1938. Experimental morphology. *In* Verdoorn, Manual of Pteridology. The Hague.

WILLIAMSON, W. C.
1871–1883. On the organization of the fossil plants of the coal-measures. Pts. 1–12. Philos. Trans. Roy. Soc. London.

WILLIAMSON, W. C., and D. H. SCOTT
1894–1895. Further studies on the organization of fossil plants of the coal-measures. Pts. 1–3. Philos. Trans. Roy. Soc. London, ser. B, 185:863–959; 186:683–702, 703–780.

ZEILLER, R.
1900. Éléments de paléobotanique. Paris.

ZIMMERMANN, W.
1930. Die Phylogènie der Pflanzen. Jena.
1938. Phylogenie. *In* Verdoorn, Manual of Pteridology.

THE SYSTEMATICS OF THE GYMNOSPERMS

By RUDOLF FLORIN
Hortus Bergianus, Stockholm

Status by the Middle of the Nineteenth Century

When A. P. de Candolle (1813) had developed his theory of the natural classification of plants on the basis of comparative and correlative morphology, great activity set in in this field. But the wealth of taxonomic suggestions was not coupled with a correspondingly deeper understanding of plant relationships. Little was yet known of the true position of the gymnosperms, or of the mutual relations of their several groups. The idea of the constancy of species was still prevalent, and taxonomy lacked the background of any evolutionary or phylogenetic theory.

A new period in the history of botany had been initiated even before 1850, *inter alia,* by the advance in microscopy and plant microtechnique. In 1842 a theory of the structure and homologies of the female conifer cones was put forward by Braun (cf. Pilger, 1926). He considered the ovuliferous scale to consist of an axillary shoot, the two lowest leaves (carpels) of which had fused, apparently forming a single organ. As regards the male conifer organs, Braun as well as Mohl (1845) stressed their character of single flowers. Brown's studies of the female organs of the conifers and cycads, and especially his opinion of their gymnospermy (1825, 1844), led ultimately to the bringing together of these plants into what was regarded as a natural group, separate from the dicotyledons. In contradistinction to the angiosperms, the conifers and cycads were supposed to have naked ovules equipped with an integument. The phyllotaxis theory of Schimper and Braun (Braun, 1831, 1835)—a characteristic product of idealistic morphology, based on the assumption of a spiral tendency in plant growth—provided floral morphology and phyllotaxis with new means of expression.

As early as 1833 Mohl demonstrated the agreement between the sporangia of the pteridophytes and the pollen-producing organs of the phanerogams, thus to some extent paving the way for Hofmeister's discoveries. Having devoted himself to the study of mature tissues, he later (1845) also explored their development. The necessity of such studies as a basis of histology and comparative morphology was emphasized by Schleiden, whose principal work (1842–1843) greatly influenced progress. Mohl was the first to investigate the development of vascular bundles and to observe cell division; he studied cell wall formation, advancing the so-called apposition theory (1853), and demonstrated (1851) in accordance with Schleiden's opinion that the cell is the primary structural element of the plant body and that this body consists wholly of cells. Nägeli (1844–1846) also contributed in laying the foundations of essential parts of cytology. According to him the growth of the cell wall is by intussusception.

Hofmeister (1849) observed that the cell nucleus may resolve itself into rod-like bodies (i.e., chromosomes). The conception of the nature and course of fertilization was at that time still fairly vague, but he was able to prove the presence of the egg cell in the ovule before fertilization, and its subsequent development into an embryo.

Hofmeister, one of the most brilliant investigators in the history of botany, did his most distinguished work in the sphere of comparative morphology (1851). He demonstrated the fundamental agreement in the life history of mosses, vascular cryptogams, and conifers. All are characterized by an alternation of generations, one spore-bearing and another exhibiting sexual reproduction. He explained how seeds are formed: the megaspore is not released from the megasporangium, but germinates there. The pollen grains correspond to the spores of vascular cryptogams. Hofmeister proved that a uniform plan underlies all cormophytes, and that the old opinion of a fundamental difference in the methods of reproduction of vascular cryptogams and phanerogams must be modified. His results supplied the basis for the distinction of five large groups of plants: Thallophyta, Bryophyta, Pteridophyta, Gymnospermae, and Angiospermae, although it was a long time before this division was accepted by systematists.

Besides these discoveries of the morphology and ontogenetic development of plants, paleobotanical research also led to some doubt of the truth of the thesis regarding the constancy of species. A real foundation of paleobotany was not laid until in the period from 1820 to about 1850. Brongniart (1849) distinguished in the historical development of the plant world three principal eras, viz., the era of the cryptogams, that of the gymnosperms, and that of the angiosperms. Floras of different characters have thus followed one another in time, and progress has—generally speaking—been from lower to higher forms. He thus helped to lay the foundations of the theory of evolution, although he himself did not draw any such conclusions. The internal structure of fossil plants was also studied to some extent (Goeppert, 1850; Williamson, 1851). Unger (1852) presented an account of the development of floras in earlier geological periods. In this he came to the conclusions that the flora of a district is not only affected by external factors, but is also changing internally, that every more recent plant species must have developed from an older, and that there is accordingly an organic connection between them.

The most important system of the conifers existing by 1850 is that of Endlicher (1847). Noteworthy features of this are that the Gnetaceae were regarded as an order of the Coniferae, that *Ginkgo* was deemed to belong to the Taxineae, another order of the conifers. The works of Endlicher and other investigators bear witness to the importance ascribed to paleobotanical research at that time in gymnosperm systematics.

The Time Up to About 1880

Darwin's *Origin of Species* (1859), which established the general theory of organic evolution, profoundly changed the point of view from which the problems of taxonomy were regarded. Fundamental agreement in structure was now explained by unity of descent, and the fact of the natural subordination of plants in groups of different orders was understood to be due to divergent evolution from a common ancestor. Classification should express not only structural resemblances, but also relationships by descent. Under the stimulus of Hofmeister's (1851) and Darwin's epoch-making works, the period saw great advances in several fields which affected the conceptions of the position and relationships of the gymnosperms. The continued progress of microscopy made possible a better knowledge of the internal structure of plants and the ultilization of such characters in taxonomy. Strasburger (1875, 1879b), who from the middle of the 1870's was the leader in the field of cytology, demonstrated that cells were formed directly out of previously existing cells, that there was no free formation of cell nuclei in Schleiden's sense, and that the nucleus could only derive from a pre-existing nucleus. Another foundation stone of modern cytology had been laid.

To Nägeli (1858) is due the credit of being the first to give an account of plant histology from the developmental point of view. He (1878) believed (cf. Hofmeister, 1867, 1868) that apical growth was fundamentally of the same nature in vascular cryptogams and phanerogams, and that it originated in an apical cell. Hanstein (1868), however, thought that in the shoot apices of higher plants growth took place in three histogenetic layers, the dermatogen, periblem, and plerome, each derived from a single cell or a group of initials. Objections to Hanstein's tissue classification were raised by Strasburger (1872), and in 1877 De Bary found the histogen theory unsatisfactory as far as the gymnosperms were concerned. Sachs (1874) distinguished between epidermal, fibrovascular, and fundamental tissues, all believed to derive from a uniform apical meristem.

Van Tieghem paved the way for a synthetic grouping of the facts relating to the primary arrangement of the vascular system of stem and root. In 1870 and 1872 he laid the first foundation of his stelar theory and pointed out that, essentially, root and stem consist of a central cylinder surrounded by a cortex. The latter is bounded on the inside by the endodermis, while the periphery of the central cylinder is marked by the pericycle bordering on the endodermis. The central cylinder is differentiated into a pith of parenchyma, differing in origin from that of the cortex, and vascular bundles separated by medullary rays.

Nägeli (1858) regarded Schimper-Braun's purely formal theory of phyllotaxis as unsatisfactory, and brought up the question of the relation between phyllotaxis and vascularization. Like him, Geyler (1867–1868) found that in conifers and related groups all vascular bundles are common to stem and leaf and join lower bundles in the stem. As to *Ginkgo,* they believed that the two strands of each leaf trace fuse into one bundle in the central cylinder, and that this bundle is then united with a lower bundle. In 1868 Hofmeister propounded a mechanistic theory of phyllotaxis which was further developed by Schwendener (1878). Mettenius (1860) examined the peculiar course of the leaf traces in stems of cycads.

A thorough investigation into the origin, structure, and activity of the cambium was carried out by Sanio (1863, 1873–1874), who, contrary to Nägeli's opinion, found that a continuous procambium ring is formed directly in the primordial meristem of the shoot apex, and further that the xylem and phloem cells in a single radial row all derive from the same mother cell. He described in detail the development of these cells and the lignification of their walls, the structure and development of the bordered pits of the tracheids, the way in which the resin canals are formed, and the structure of the early and late wood.

Other contributions to the knowledge of gymnosperm anatomy concerned the mode of formation of new cells in meristems and the arrangement of their walls; the origin of primary xylem and phloem; the tracheids in primary and secondary wood and the nature and development of their pitting; the secondary phloem; the stomata, transfusion tissue, secretory organs, and crystalline deposits of calcium oxalate in leaves, etc. Attempts had earlier (Goeppert, 1850) been made to utilize the characters of the secondary wood as an aid in characterizing conifer genera, but systematic plant anatomy did not become a more prominent branch of botany until in the 1870's. The most important work in this field is C.–E. Bertrand's (1874) comparative study of stem and leaf anatomy. The anatomy of vascular plants in general was summarized by De Bary (1877).

As to the reproductive organs, the interpretation of the morphology of the male flowers generally met with no great difficulties. The pollen grain was recognized as a microspore, the pollen sac as a microsporangium, the "stamen" as a microsporophyll (Warming, 1873, 1877), and the aggregation of microsporophylls on an axis as a flower (Eichler, 1863; Strasburger, 1872). Opinions differed, however, on the male flowers of the Gnetaceae (Strasburger, 1872; McNab, 1873; etc.). This applies even more to the female organs—except to those of the cycads, which were interpreted as single flowers with ovules marginally attached to open carpellary leaves (Miquel, 1869; Tieghem, 1869; Braun, 1876; Warming, 1877). The conifer cones in particular were debated. Their correct interpretation was considered an essential prerequisite for a determination of gymnosperm relationships.

The axillary ovuliferous scale of the Pinaceae was in Braun's (1860) opinion a fertile, two-leafed short shoot or flower with the leaves fused along their posterior margins. *Taxus* and *Ginkgo* lacked ovuliferous scales. The *Araucaria* cone scale was formed by the fusion of a single-leafed short shoot to the bract, while the flower of the Taxodiaceae, and probably also of the Cupressaceae, had several small leaves fused together and to the bract. Baillon (1860, 1864) definitely opposed Brown's thesis of the gymnospermy of the conifers and taxads. According to Baillon the female flower is either terminal, or placed in the axil of a bract or leaf, but always borne on an axis. It is not gymnospermous, but possesses two carpels and a naked ovary containing an erect, orthotropous ovule upon a basal placenta. Baillon's account was criticized by Caspary (1860), who interpreted the so-called ovary as an ovule, the two "carpels" as a two-lipped integument, and the ovuliferous scale of the Pinaceae as formed by the two first leaves of an axillary short shoot fused along their anterior margins. Eichler (1863) attributed to the naked ovules of the conifers a single, or sometimes double, integument. The ovules were in certain cases covered by an aril, but never by an ovary or a perianth, and they were borne in the axils of small leaves on a rudimentary short shoot, placed in its turn axillary to a bract. Sachs (1868), however, wanted to regard the ovuliferous scale of the Pinaceae as an excrescence on the bract, and the bract as a carpel. In 1869 van Tieghem threw fresh light on this problem from the point of view of comparative anatomy. In the ovuliferous scale of the Pinaceae the bundles were inverted as compared with those of the bract and foliage leaf. Even the apparently single cone scale of the Cupressaceae had such a double-bundle system. The conifer ovules are in his opinion attached to the underside of the first and only leaf of a reduced axillary shoot. This leaf, which turns its ventral side towards the bract, is an open carpel representing the whole female flower. Mohl (1871) regarded the double needle of *Sciadopitys* as analogous with the ovuliferous scale of the Pinaceae, which he interpreted in accordance with Braun's original conception. Strasburger (1872), on the other hand, repudiated Brown's theory of the gymnospermy and believed that the conifers had female flowers in the form of ovaries. These were metamorphosed buds, in which the tip of the axis was changed into a nucellus. The wall of the ovary was formed by two carpels fused along their margins. Both Braun (of late years) and he were of the opinion that the conifer ovule is a metamorphosed shoot or flower, and that the ovuliferous scale, with its ovules, constitutes an inflorescence in the axil of the bract (cf. Eichler, 1875). But, abandoning his objection to gymnospermy, Strasburger later (1879a) came to regard what had been designated ovaries as naked ovules. In the Pinaceae, the ovuliferous scale is a two-flowered inflorescence consisting of one primary and two secondary shoots, the latter represented by the ovules. The female cones of this family were also dealt with by Stenzel (1876), Čelakovský (1879), and Willkomm (1880), who all considered the conifers as gymnosperms, and the ovuliferous scale to be formed by two carpellary leaves fused along their posterior margins, i.e., by the two prophylls of a reduced and metamorphosed axillary shoot (brachyblast), each bearing an ovule on its underside. While the problem of the gymnospermy had on the whole been settled in favor of the opinion of Brown, no unanimity had been reached on the structure of the female conifer cones in spite of intensive research, a circumstance which greatly affected gymnosperm taxonomy. The morphology of the female reproductive shoots of *Ginkgo* and the chlamydosperms was also disputed.

Much work was done in order to elucidate the formation of microspores and megaspores, the development of the gametophytes, the mechanism of pollination, the fertilization, and the embryogeny, of the gymnosperms. Hofmeister (1858) had already compared the modes of fertilization and the development of the female gametophytes in several groups of vascular plants. Most work was, however, done by Strasburger (1872, 1878, 1879a), who dealt with conifers, taxads, *Ginkgo,* and chlamydosperms. The generally wind-borne pollen grains were considered to contain the last remains of the prothallial tissue of the vascular cryptogams and a strongly reduced antheridium. Male gametes were formed in the pollen tube. He also demonstrated the reduction of the neck of the archegonium, and its still remaining ventral canal cell or nucleus, as well as that fertilization consisted in the fusion of two gametes. The fertilized egg nucleus was not dissolved, as previously believed, but immediately began to divide to form the cells of the proembryo. Strasburger presented the most monumental contribution of all early workers on gymnosperm embryology.

The general adoption of the doctrine of evolution, and the development of microscopy opened a new flourishing period in the history of paleobotany. The most prominent paleobotanists of that time were Williamson and Renault. From 1871 onwards, Williamson published a long series of important monographs on the structure of vascular plants of carboniferous age. Calamites, sigillarias, and lepidodendrons presented secondary growth, and were therefore thought to be gymnosperms. Williamson proved, however, that this is only a subordinate character, and that the said plant groups are actually vascular cryptogams. Renault, who with Williamson may be considered a founder of modern paleobotany, also devoted himself mainly to microscopic examinations of paleozoic plants. In this connection his study of the cordaites (1879) attracts most interest. In 1877 Grand' Eury had given an account of this extinct group. Renault investigated the stem, root, and leaf anatomy, the morphology of the male and female inflorescences and of the pollen, and the anatomy of the seeds (cf. Brongniart, 1881). While Grand' Eury had considered the cordaites most closely related to the conifers, Renault believed that they formed a separate group of cycads. He also described the stem anatomy of the Poroxyleae, a new group of fossil gymnosperms.

The stems of *Medullosa* were investigated by Goeppert and Stenzel (1881), and were believed to represent a new group of fossil cycads. Kraus (1870–1872) divided recent and fossil conifer stems into five groups, viz., *Araucarioxylon, Pityoxylon, Cedroxylon, Cupressinoxylon,* and *Taxoxylon,* a classification which for a time became generally adopted by paleobotanists. Carruthers (1870, and earlier) studied the presumed cycad genera *Williamsonia* and *Bennettites* of mesozoic age, and Schenk (1867) began the microscopic study of fossil plants preserved as compressions.

Evolutionary ideas, and the results of morphological and anatomical research, were only gradually expressed in the classification of gymnosperms. The old system of A. P. de Candolle (1819) was essentialy the basis of that of Bentham and Hooker (1880). Braun (1864) was the first to place the gymnosperms as an independent group between archegoniates and angiosperms; he distinguished three families: Cycadaceae, Coniferae, and Gnetaceae. Eichler (1880) then divided the conifers into the Taxineae (including *Ginkgo*), Cupressineae, and Abietineae. Important works on the classification of the cycads were presented by Miquel and Regel (Schuster, 1932). A distinguishing feature of the gymnosperm systems of the period now reviewed is that the extinct fossil groups are disregarded.

The Period 1880–1900

Ever since Hofmeister's work of 1851, the alternation of generations in cormophytes had been in the foreground of the general botanical interest. Čelakovský (1874) had distinguished between homologous and antithetic alternation. The former implied a differentiation of generations of fundamentally like descent, while the latter was characterized by an intercalation of a new—sporophytic—stage between successive gametophytes. Bower (1890, 1894) became the chief exponent of the antithetic theory. His view was supported by the discoveries of Overton and Dixon that the nuclei of the cells of the gametophytes in gymnosperms have only half as many chromosomes as the sporophyte. Strasburger (1894) considered this difference fundamental.

The development of the gametophytes was gradually elucidated. Belajeff's investigations (1891, 1893) of the male gametes in *Taxus* and conifers were an important advance. Strasburger (1884, 1892) confirmed in the main his account for all the principal gymnosperm groups, and proved that a mature pollen grain of the Pinaceae and *Ginkgo* as a rule contains, in polar arrangement, two prothallial cells, one antheridial cell, and the vegetative pollen-tube cell, while *Taxus* and Cupressaceae lack prothallial cells.

The discovery by Hirase (1895, 1898) that the *Ginkgo* ovules are fertilized by motile ciliated sperms caused a great sensation. Strasburger (1892) described the differentiation of the pollen tube into a rhizoidal and a generative part, which also separates *Ginkgo* from the conifers. The formation and subsequent development of the pollen grains in the cycads had already been examined, but Ikeno (1898) was the first to give a full account of the development of the male gametophyte (*Cycas*) and to demonstrate that, here too, the male gametes were spermatozoids with bands of cilia developed from blepharoplasts. The occurrence of spermatozoids in *Zamia* and *Stangeria* was announced by Webber (1901) and Lang (1900) respectively. These discoveries are remarkable events in the history of plant morphology.

It was known that the pollen grains, like the spores of the vascular cryptogams, were formed by tetrad division of mother cells associated with a reduction of the chromosome number. Juel (1900) found that in *Larix* the megaspore mother cell is homologous to the microspore mother cell, and divides in the same way. In the gymnosperms, only the chalazal megaspore generally develops into a prothallium. The cell formation in the female gametophyte of taxads, conifers, and ephedras was described by Sokolowa (1891), and several other works on the development of the female gametophyte and the archegonium were published. The ventral canal cell or nucleus was interpreted as an arrested gamete. Conditions in *Gnetum* (Lotsy, 1899) proved to differ from those in other gymnosperms by the lack of archegonia and in other ways.

The nuclear divisions in tissue cells and spore mother cells, and the fertilization process were investigated. Strasburger and his students laid the foundations of karyology. The problem of reduction division came increasingly to the fore, and the first observations of the chromosome numbers of plants were made. As to the shoot apex, Koch (1891), and others, found that Nägeli's apical cell theory was not applicable to gymnosperms. Nor had Hanstein's histogen theory proved tenable.

Van Tieghem (van Tieghem and Douliot, 1886, 1888; van Tieghem, 1891a, 1898, etc.) further developed his stelar theory. Sachs's (1874) classification of tissues was increasingly displaced by the new division into epidermis, cortex, and stele, which applied to stem, root, and leaf. The primitive type of central cylinder, the monostele, consists of a single concentric fibrovascular strand, bounded externally by the pericycle. It may become polystelic by dichotomy. It may also expand and develop a central pith and radiating medullary rays. In the latter case the endodermis and pericycle may become folded in between the bundles, uniting at the inner side of each. This astelic type may in addition be modified by the separate bundles uniting into a more or less complete ring, bounded by a continuous pericycle and endodermis (gamodesmic stele). The steles of the polystelic axis may in their turn form a concentric annular stele (gamostele). The stele concept was universally accepted. Strasburger (1891) did not think that astelic axes differed in principle from monostelic. More important was that van Tieghem's opinion on the origin of polystely proved to be incorrect.

Later Jeffrey (1899a–1899b) propounded a modified stelar theory, distinguishing two basic types of structures, viz., the single solid concentric strand without any pith, the protostele, and the concentric fibrovascular tube perforated by gaps and including a central pith, the siphonostele. There were two types of siphonosteles, viz., the amphiphloic, with external as well as internal phloem, and the ectophloic, with only external phloem. When the gaps of the stelar tube correspond to leaf traces, as in the gymnosperms, the siphonostely is phyllosiphonic, and when there are no foliar gaps it is cladosiphonic. Jeffrey derived the siphonostele from the protostele, and thought that the pith was, phylogenetically, formed by invasion of cortical tissue into the stele.

The study of gymnosperm vegetative anatomy progressed actively also in other directions. Investigations concerned the pith of the stem, the phloem, the wood rays, the tracheid walls with their bordered pits, the trabeculae in secondary wood, the behavior of the leaf traces, and the resin ducts in roots, stems and leaves. Penhallow (1896) and Kraus (1886), studied the secondary conifer wood for the purpose of defining genera and species and of establishing the relations to fossil woods.

The cycads attracted much attention from the phylogenetic point of view (cf. Strasburger, 1891). Solms-Laubach (1890a) demonstrated the position of the cones and the sympodial nature of the stem. The complicated course of the leaf-trace bundles was found to change in the peduncle of the cone into a simplified organization conforming to conditions in the bennettites. Scott (1897) concluded from a comparison with certain Cycadofilices that the mesarch cycadean type of vascular bundles represents a vestige of a primitive organization that was once common to leaf and stem. Worsdell (1898a, 1898b, 1901) found two types of stem structure in cycads, viz., one in which there is a single stele and another in which there is more than one cylinder. He derived the vascular tissues of the cycad stems from those of the paleozoic Medullosaceae, while according to Scott (1899) the primary ground plan of the stem structure of a polystelic *Medullosa* is fundamentally different from that of monostelic cycads.

In his comprehensive account of gymnosperm anatomy, Strasburger also dealt with the leaves particularly as regards the vascular bundles and the origin of leaf traces. Other botanists studied the stomatal apparatus in conifers, their trichomes, and the general anatomy of juvenile and adult leaves. A good deal of attention was given to the transfusion tissue. According to one view, this tissue forms part of the conducting tissues to the vascular bundle. Others thought that it belonged to the parenchymatous tissue of the leaf, while according to van Tieghem (1891b) it is a part of the pericycle of the bundle. Worsdell (1897) tried to prove that the transfusion tissue is, phylogenetically, a direct derivative of the centripetal xylem, which normally occurred in primitive extinct gymnosperms, and is still found fully developed in the adult cycad leaves and in the cotyledons of *Ginkgo*.

Bower (1885) treated the leaf as a potential branch system, and used the term phyllopodium for its axis. This axis may develop in various ways without branching, or it may produce simple or ramified branches. The simultaneous progression of the arrest of the apical growth of the phyllopodium in large-leaved vascular cryptogams and gymnosperms, and of the tendency of the pinnae to develop in a basipetal succession, pointed to these phenomena being mutually connected.

Thibout (1896) investigated the morphology and anatomy of the male organs and distinguished two main types of organization of the microsporophyll, viz., the leaflike, hyposporangiate cycadean type and the stalklike acrosporangiate gnetalean type. Lotsy (1899) believed that the Gnetales (chlamydosperms) are equivalent to all other gymnosperms, and to the angiosperms, and of entirely independent origin.

The debate on the morphology of the female reproductive shoots in conifers, taxads, and *Ginkgo* continued. The leading investigator was now Eichler (1881, 1882a, 1882b, *in* Engler and Prantl, 1889), who, changing his earlier opinion, adopted Sachs' view of 1868. The cone scales of all conifers are nothing but open carpellary leaves, and the ovuliferous scales, where present, ventral excrescences (ligulae, placentae) on these. Delpino (1889) and Penzig (1894) rejected Eichler's interpretation, and instead thought that the ovuliferous scale had arisen by the fusion of two lateral lobes of the bract. At first Čelakovský (1882a, 1882b), conceded that the ligule of *Araucaria* might be regarded as an excrescence on a carpel, but in 1884 he recanted this opinion and interpreted the *Auraucaria* cone like those of the Pinaceae. In view of the increasing fusion of the bract to the ovuliferous scale, which is composed of carpels, he assumed that the Pinaceae, Taxodiaceae, Cupressaceae, and Araucariaceae constituted a phylogenetic series. In the taxads the ovule was displaced from the axil to the apex of the uppermost leaf on the fertile short shoot. In 1890 (1898, 1900) Čelakovský stressed that ontogeny and teratological cases had undoubtedly proved the ovuliferous scale of the Pinaceae to be a short shoot. In the main, it is reduced to two fertile, collaterally fused uniovulate carpels turning their ventral sides towards the bract, and a sterile leaf, usually aborted, but in the pine united with the carpels to form part of the ovuliferous scale. The female conifer cones were also anatomically re-examined, particularly by Radais (1894) and Worsdell (1899, 1900b). The latter finally (1900a) published a historical study showing that the nature of the female reproductive parts of the conifers and taxads remained the same unsolved problem as it was at the very beginning of the nineteenth century. The female reproductive complex of *Ginkgo* and *Gnetum* was also disputed. (Čelakovský l.c., Lotsy 1899). The old question of the nature of the ovule and its integument is intimately connected with these problems.

Paleobotany made considerable progress in the period under review (Scott, 1900). The existence of a paleozoic group of plants, apparently combining characters of ferns and cycads, had been recognized for some time. Grand' Eury (1877) and Renault (1883) established the close similarity between the petioles of the large fernlike fronds of *Alethopteris* and *Neuropteris* preserved as impressions and the detached petioles known structurally by the name of *Myeloxylon*. Schenk (1889) and Weber and Sterzel (1896) proved that the *Myeloxylon* type of petiole had been borne on *Medullosa* stems. The foliage of medullosean stems was therefore—at least partly—of the *Alethopteris* and *Neuropteris* types.

Stur (1884) excluded these from the ferns and referred them to the cycads. Williamson and Scott (1896) studied the stem anatomy of *Heterangium* and *Lyginodendron* and concluded that they united the characters of ferns and cycads. On the basis of these facts, H. Potonié (1897–1899) applied the name Cycadofilices to this transitional group of vascular plants. Finally, Scott (1899) examined the structure of a *Medullosa,* which represented the genus in its simplest expression. Its stem was polystelic, each of the three pithless steles resembling the single central cylinder of a *Heterangium,* and covered by the bases of the petioles of *Alethopteris* fronds. The Poroxyleae, another group of extinct gymnosperms apparently related to both the Cycadofilices and the cordaites, were further investigated by Bertrand and Renault (1884–1887, 1889) and Renault (1896), and found to be of significance in the discussion of the derivation of the higher gymnosperms.

The Mesozoic era had become known as the "Age of the Cycads." On closer examination, however, the reproductive organs of the fossils mostly proved quite different from those of present-day cycads. Our knowledge of the bennettites was considerably enriched by Solms-Laubach (1890b), Scott (1900), Lignier (1894), and Wieland (1899, 1901). The bennettites resembled the true cycads in many ways, but their leaf-trace bundles had a much simpler course, the woolly hairs were replaced by ramenta like those of ferns, the fertile shoots were axillary, and the reproductive organs quite different. The apex of the fertile shoot was modified into an ovuliferous receptacle enveloped by pinnate bracts and carrying seed pedicels, each with a terminal orthotropous ovule, intermingled with interseminal scales. A dicotyledonous embryo almost filled the cavity of the seed. Wieland recognized the microsporophylls, which were pinnately compound, synangia-bearing organs, united at their bases to form a sheath. The "flowers" were bisexual, and had a verticil of microsporophylls inserted below the base of the ovuliferous receptacle. The discovery of this group is one of the most important advances in the history of paleobotany.

The phylogeny of gymnosperms and the question of the monophyletic or polyphyletic origin of the group were discussed, and a variety of views put forth. The scheme proposed by Engler (Engler and Prantl, 1897) marks a distinct advance in the direction of a phylogenetic system of the gymnosperms. It included no less than six classes, viz., the Cycadales, Bennettitales, Cordaitales, Ginkgoales, Coniferae, and Gnetales, but the Cycadofilices were not yet taken into consideration. The heterogenous nature of Engler's Taxaceae and Gnetaceae was not realized until much later, and the interrelationships of the Pinaceae remained little understood.

The Period 1900–1930

This period was characterized by greatly increased activity in most fields, and by several discoveries of fundamental importance. Speaking generally, the most important of the latter was the sensational rediscovery in 1900 of Mendel's till-then-neglected laws of heredity, formulated in 1865. This initiated a magnificent progress of genetics. The concurrent advances in cytology and the association of this branch with genetics eventually led to studies of the evolution of species in various plant groups. The gymnosperms played a subordinate part, however, as objects of investigation in this connection. The subject of "macroevolution" is moreover hardly approachable by means of the experimental methods of genetics.

Bower (1908) further developed the antithetic theory of the alternation of generations, according to which the neutral generation would be a new product with a phylogenetic history of its own. The ultimate origin of all the vegetative tissues of the sporophyte in the Cormophyta was the sterilization of potentially fertile cells. Attention was subsequently especially directed to conditions in the lower cryptogams, which led to the difference being stressed between the alternation of nuclear phases on the one hand, and of morphological generations on the other. Kidston and Lang (1921) stated that the morphology of the Devonian psilophytes did not entirely support either the homologous or the antithetic theory. The simple sporophyte of *Rhynia* was part of an antithetic life history, while its organization could be treated as homologous to the plant body as realized in the sexual as well as in the spore-bearing stages of many algae.

The fundamental organization and evolutionary development of the sporophyte was more eagerly discussed than ever before, and a good many theories were propounded in explanation of the relationships of stem and leaf (Rudolph, 1921; Chauvead, 1921). Most of these may be passed over here. In continuing his investigations on stelar structures, Jeffrey (1902, 1910; cf. Worsdell, 1902a; Schoute, 1903) divided vascular plants into two great stocks: the Lycopsida—cladosiphonic and palingenetically microphyllous—and the Pteropsida—phyllosiphonic and palingenetically megaphyllous—the latter including ferns, gymnosperms, and angiosperms. The concentric type of siphonostele was regarded as more ancient than the collateral and the primary bundle system of the vascular plants to present a reduction series, of which the earlier and more complex stages were found in ferns and lower gymnosperms and the more recent and simplified stages in the higher gymnosperms and the dicotyledons. A stelar terminology was elaborated (Brebner, 1902; Zimmermann, 1930), but no scheme became generally accepted; Meyer (1917) definitely opposed the stelar theory.

Jeffrey's classification of the vascular plants was criticized by Tansley (1908), who pointed out that many of the modern microphyllous forms appeared to be reduced derivatives of megaphyllous ancestors and that the Lycopsida could not all be considered palingenetically microphyllous. It was realized that the formation of leaf gaps in the stele was not an absolute criterion of the morphological nature of the leaf. The whole question appeared to Tansley to resolve itself into the actual size relation of leaf-trace to stele, as modified by the ancestrally determined construction of the latter. Bower (1908) expressed similar views. At the beginning of the century all seed plants were considered to have originated from vascular cryptogams, and the Cycadofilices to be actually derived from ferns. The centripetal xylem was characteristic of the primary bundles of both pteridophytes and seed plants although it was gradually reduced and finally disappeared in the stem of the latter (Scott, 1902). The views of the relationships of the Cycadofilices subsequently changed, and it was admitted that they differed from the ferns not only in their reproductive organs, but also in essential features of their anatomical structure (Scott, 1923; Posthumus, 1924). The assumption of a close affinity between these two groups as expressed in the phylum Pteropsida had to be given up; Jeffrey's idea of a common megaphyllous origin of the gymnosperms was rejected.

Lignier (1908–1909; cf. Bugnon, 1922) also considered the leaves of the vascular plants to be diphyletic. The simple uninerved leaves of his Phylloideae were thought to be of the nature of emergences, while those of his Phyllineae were dichotomized and cladodified cauloids. The Phyllineae had developed in different directions. In the Macrophyllineae, comprising ferns, pteridosperms, and cycadophytes, the leaf dominated the axis. In the Microphyllineae, comprising cordaites, ginkgoes, and conifers, the axis had got the upper hand of the leaf, and was more branched. An intermediate position was taken by the Mesophyllineae or angiosperms. The grouping of the gymnosperms corresponds to Sahni's (1920) later division of them into phyllosperms with leaf-borne seeds, and stachyosperms with stem-born seeds. Lignier's theory produced various further contributions to the debate (Florin, 1938–1945).

The overtopping theory of H. Potonié (1912) explained the leafy shoots of the higher plants as derived from the dichotomously ramified thallus of algal plants. Overtopping branches formed between them the axis, with infinite apical growth, while the leaves, of finite growth, originated from weak overtopped branches or branch systems of the thallus. Axis and leaf would thus be morphologically equivalent organs of common origin. Kidston and Lang's aforementioned studies of the psilophytes profoundly influenced the fundamental conceptions of shoot, axis, leaf, and sporophyll in vascular plants. The plant body in general now appears to be a simply or complexly branched axis; the so-called fundamental organs are merely parts of this system, specialized for various functions. Their discoveries induced Zimmermann (1930) to coordinate the new morphological ideas into the telome theory, which became of great interest in connection with the problem of the early evolution of the gymnosperms.

Worsdell (1902b) summarized the theories of the nature of the ovular integuments. According to the foliar-appendage theory, they are foliar appendages of the axial nucellus. The *sui generis* theory regards the integuments as outgrowths of the sporangium, an organ *sui generis.* According to the foliolar theory, they are the morphological homologues of a three-lobed segment of the megasporophyll (carpel). On the basis of the seed structure in cycads and Cycadofilices, Benson (1904) then advanced the theory that the seed is a synangium, in which the peripheral sporangia have been sterilized and specialized as an integument enveloping the single fertile sporangium. De Haan (1920) reviewed the whole subject, and suggested that in gymnosperms the integument is formed by collateral fusion of a varying number of equivalent elements. In 1927 Thomson discussed the evolution of the seed habit in plants on the basis of the sizes of megaspores and microspores at a stage when they have not yet been enlarged to accommodate the prothallium. He found that "heterangy in combination with homospory and heterothally forms the distinctive features of the seed habit, while heterospory represents the culmination of the free-sporing habit."

With a view to the phylogenetic relations, anatomy in general—and especially the vascular system—was more intensely investigated than before. Attention was paid to the structure of both the adult and seedling stages. New discoveries made the importance of paleobotany increasingly clear, and it was realized that the results of comparative anatomical research on living and fossil forms must play an important role in any scheme advanced. Since Hofmeister, and especially Strasburger, had laid the foundation of our knowledge of the gametophytes, fertilization, and embryo formation, and the spermatozoids of *Ginkgo* and cycads had been discovered, this branch of research attracted great interest.

Numerous progressive series were worked out, showing more or less graduated changes in various organs, and Zimmermann (1930) emphasized the importance of the study of "phylogeny" of single characters. Great expectations were attached to the new serodiagnostic method (Mez, 1926), the object of which was experimentally to elucidate the relationships of the various plant groups, but they were hardly fulfilled (Wettstein, 1925; Gilg and Schürhoff (1927).

Interest was centered about 1870 and 1880 on meristem research, but this was for a long time displaced by research in other directions. In 1926, however, Schüepp summarized our knowledge of apical growth. Jeffrey (1917) treated the anatomy of the woody plants with special reference to its historical and experimental aspects. Great stress was laid on three "canons" of comparative anatomy which, however, were all more or less open to criticism:

1. The doctrine of recapitulation of the history of the race in the development of the individual.
2. The doctrine of conservative organs (leaf, reproductive axis, root, the first annual ring of the stem, and sporangium).
3. The doctrine of reversion, an expression used for certain effects of wounding believed to be reminiscent of ancestral characters.

As regards tissue systems, Sachs's old divisions were reaccepted by Jeffrey as a consequence of the theory of the common origin of pith and cortex. In discussing the evolutionary tendencies of gymnosperms, Coulter and Chamberlain (1917), following Jeffrey, emphasized the evolution from the protostelic condition to the siphonostelic. The universal tendency was to eliminate the centripetal xylem until the collateral mesarch bundles became collateral endarch, first in the central cylinder, and finally also in the peripheral regions. The transfusion tissue was especially studied by Bernard (1904); his conclusions came very close to those of Worsdell (1897), but he went still further, and considered this tissue to be actually centripetal xylem. Other investigators maintained that it arises independently of the centripetal wood. Porsch (1905) and Rehfous (1917) investigated the stomatal apparatus of the gymnosperms from the evolutionary point of view. Hill and De Fraine, (1913; cf. Dorety in Coulter and Chamberlain, 1917) found that details of seedling anatomy are apparently not of any great help in instances of questionable relationships between two plants or plant groups. Finally, Eames and MacDaniels (1925) treated the current status and opinion of general plant anatomy.

Intense cytological activity gradually led to the revelation of, *inter alia,* the constancy of the chromosome number in the organism and its importance as a systematic criterion. The following seem to have been the only certainly known haploid numbers at the end of the period: *Ginkgo* 12, *Pinus* 12, *Larix* 12, *Tsuga* 12, *Picea* 12, *Podocarpus* 12, *Cephalotaxus* 12, *Juniperus* 11, *Taxus* 12, and *Ephedra* 7. The uniformity of conifer karyology appeared remarkable. Of other events we need only mention that the first decade of this period was characterized by much work to elucidate the meiotic division.

The leading position in gametophyte research after Strasburger was taken by Coulter and Chamberlain (1917) at the head of the Chicago school of botanists. Their results have had a great share in modifying our ideas of the phylogeny of the several groups. Summaries were also published by Schnarf (1933) and Chamberlain (1935). It was established that in the male gametophyte there has been a tendency to reduce the number of cell divisions. Types of pollen in which prothallial cells are formed are considered more primitive than those where such cells do not occur. In cycads, as well as in *Ephedra* and probably also *Welwitschia,* there is only one prothallial cell. *Gnetum* appears to have only a prothallial nucleus, but in *Ginkgo* and the Pinaceae there are two of these cells, while in most of the remaining conifers and in the Taxaceae they are eliminated. The Araucariaceae and Podocarpaceae generally have two prothallial cells in the mature pollen grain, but these sometimes divide secondarily to form many-celled tissue. Only two male gametes are as a rule produced in the pollen tubes. A noteworthy exception was discovered by Caldwell in *Microcycas,* where 8–10 spermatogenous cells are always formed instead of one, and the number of spermatozoids is increased correspondingly. The stalk cell formed by the division of the antheridial cell has apparently retained its original function as a spermatogenous cell and its capacity to divide. The two male gametes of the higher gymnosperms are either highly organized cells, or have lost their cell walls. The taxads show reduction in the direction of the elimination of one of the two gametes.

The development of the female gametophyte has been found to be marked by a period of free nuclear divisions followed by a period of wall formation. *Welwitschia* and *Gnetum* differ in a remarkable manner from all other gymnosperms. In the typical gymnosperms the main feature is the reduction of the archegonium. The differentiation of a definite ventral canal cell as in *Ginkgo* and the Pinaceae is a primitive feature. In the majority of the cycads and conifers, wall formation has been entirely eliminated between the egg and ventral canal nucleus. A neck canal cell is not found; the two-celled neck, which occurs in the cycads and *Ginkgo,* is probably primitive, while the many-celled neck of *Ephedra* appears to be an advanced feature. The numbers and arrangement of the archegonia vary considerably. The condition in most cycads, where a limited number of archegonia occur free from one another in the micropylar end of the gametophyte, is looked upon as relatively primitive, while the spreading of the archegonia over a larger part of the gametophyte and the formation of archegonial complexes—which both occur in the Taxodiaceae and Cupressaceae—are considered advanced features.

Knowledge of the external structure of the megaspores and microspores was also furthered. According to Thomson (1905) a megaspore membrane is present in all gymnosperm groups. From the point of view of the relative development of this coat and the tapetum he concluded that the Pinaceae, as well as some forms of the Taxodiaceae and Podocarpaceae, form ancient groups, and the taxads the most recent group. The number and arrangement of the places of exit on the surface of the pollen grains were investigated by Pohl (1928) and Tammes (1930). The basic type in the gymnosperms is furnished with a single longitudinal fold or germinal furrow at the distal pole, and occurs in the cycads, *Ginkgo,* Pinaceae, and *Podocarpus.* When two air sacs occur, they are situated on either side of this fold. The microspores of *Taxus* and *Juniperus* represent a reduced form.

Burlingame (1915a; cf. Goebel, 1932; Schnarf, 1933) distinguished four methods of pollination and fertilization in gymnosperms:

1. In the extinct Cycadofilices and cordaites the pollen grains lodged in a pollen chamber in the nucellus, and probably did not develop pollen tubes.
2. In the cycads and *Ginkgo* they lodge in a pollen chamber in the nucellus, and form haustorial branching pollen tubes, which do not penetrate towards the female gametophyte or take any part in transferring the ciliated sperms to the archegonia.
3. In most of the conifers the pollen passes down to the tip of the nucellus, where it puts out a pollen tube as a sperm carrier.
4. The araucarians are pollinated on the ovuliferous scale at a distance from the ovule, from which point a pollen tube grows towards the micropylar end of the ovule and there enters the protruding nucellus.

Coulter and Chamberlain in 1917 gave an account of the rather meager knowledge of gymnosperm embryogeny at that time. The real advance in this field is mainly due to Buchholz (1929), who in 1918 began publishing a series of contributions relating to the conifers. Considering mainly the early stages between the proembryo and the organization of the embryo into tissue regions and organs, Buchholz realized that many of the diverse features of conifer embryogeny are variations due to the complications of cleavage (monozygotic) polyembryony, a condition occurring, together with simple (polyzygotic) polyembryony, in this group, in contradistinction to that of the cycads, where only the latter type of polyembryony is found. He regarded as primitive features an extended period of apical cell growth in the embryo, cleavage polyembryony, and rosette embryos. The absence of apical cells, simple embryogeny, the absence of rosette cells, and the presence of embryonic caps, were believed to represent the most advanced features of conifer embryogeny.

Pteridospermae

One of the most important events in the history of paleobotany was the first recognition of the seed of a member of the paleozoic Cycadofilices. This seed, *Lagenostoma Lomaxi,* was enclosed in a cupule bearing capitate glands identical in form and structure with the glands on the associated vegetative organs of *Lyginopteris* (*Lyginodendron*) *oldhamia* (Oliver and Scott, 1904). The seed, of complex structure, is orthotropous, radially symmetrical, and borne terminally on the ultimate and naked ramifications of the frond. The group name Pteridospermae was introduced, and later (Scott, 1923) proposed for exclusive use in place of the name Cycadofilices. In 1904 White announced the terminal attachment of small seeds to pedicel-like pinnules of the frond of *Aneimites fertilis,* and in 1905 Grand' Eury published his find of similar seeds on the frond of *Pecopteris Pluckeneti,* where they occurred at the margins of almost unmodified pinnules. Kidston (1904) found large seeds attached terminally to a pinna rachis of *Neuropteris heterophylla.* In 1911, Kidston and Jongmans described the even larger seed of *Neuropteris hollandica.* Much indirect evidence was brought to light, from association and comparative structure, in support of the assumption that such frond genera as *Neuropteris, Alethopteris, Lonchopteris,* and *Linopteris* represented pteridosperms with medullosean stems, and with seeds of the *Trigonocarpus* or related types. Further instances of seeds attached to fronds of *Sphenopteris* were observed, but the most significant contribution in recent years was made by Halle (1929), who studied no less than five new cases of seed-bearing fronds, viz., one species of each of the genera *Sphenopteris, Pecopteris, Alethopteris, Emplectopteris,* and *Nystroemia.* Halle got the impression that a terminal position of the seed was the rule among the older pteridosperms, and that marginal and laminar attachments did not appear until later. It seemed likely to him, therefore, that the seed habit originated in plants which still had terminally placed sporangia. Much work was also devoted to the elucidation of the internal structure of various paleozoic seeds, found only detached, but believed to belong to pteridosperms (Scott, 1923). They differ in size and symmetry, in the structure of the testa, and in the organization of the nucellus and the integument in the micropylar region.

The male organs of *Lyginopteris oldhamia* are still not known with certainty, but Benson (1904), Crookall (1930), and others, have suggested that *Telangium Scotti* might be its microsporangia. It proved difficult in many cases to differentiate pteridosperms from marattiaceous ferns (Kidston, 1923–1925). Some plant remains were believed to represent male organs of the Medullosaceae, but the situation was far from satisfactory, and it was not until after the end of this period that better knowledge was gained.

Research on the vegetative anatomy of the pteridosperms made further progress (Scott, 1923). This applies, *inter alia,* to the Calamopityaceae, which were grouped with the pteridosperms entirely on the basis of their stem structure and regarded as being, at least in part, most closely related to the Lyginopteridaceae. As regards the Medullosaceae, *Sutcliffia* indicated the probable derivation of the complex, polystelic, medullosean stem from a simple, solid, protostelic type, such as existed in *Heterangium.*

The old conception of the filicinean origin of the seed plants—which can be traced back to Hofmeister's time—had had to be abandoned. The pteridosperms and the contemporary ferns came to be regarded as distinct and in some respects parallel series.

Caytoniales

In 1925 Thomas discovered in rocks of mesozoic age remains of a new group of seed plants, which he named the Caytoniales. The remains consisted of fruit-bearing stalks interpreted as pinnate megasporophylls (*Caytonia*), also branched microsporophylls bearing quadrilocular sporangia in terminal clusters on each subdivision, and palmately compound leaves (*Sagenopteris*). On each pinna, the megasporophyll bears an almost closed, saclike body containing several seeds; the testa is of three-layered complex structure. The pollen grains possess two wings placed opposite each other. Thomas believed that the Caytoniales occupied a position between the paleozoic pteridosperms and the recent angiosperms, but their supposed affinities with the latter group were doubted by the majority of paleobotanists.

Cycadales

The study of the cycads was greatly promoted by Coulter (Coulter and Chamberlain, 1917), and especially by Chamberlain (1935), not only in respect to gametophytes, fertilization, and embryogeny, but also as regards the external morphology and anatomy in general of their reproductive and vegetative organs. Chamberlain, Goebel (1923), and Pilger (1926) traced a gradual reduction from *Cycas revoluta* to *Zamia*, in the size, form, and branching of the megasporophylls, in the number of ovules, and in the number of microsporangia on each microsporophyll. Stopes (1904) thought that the cycad ovules had a double integument, but Quisumbing (1925) showed that this was an error due to the failure to study the stony layer of the testa from its inception. According to Kershaw (1912) the closest parallel to the cycads among fossil seeds is to be found in those of *Trigonocarpus* affinity.

The bulk of the secondary xylem in cycad stems consists as a rule of tracheids with multiseriate bordered pits, but in *Stangeria* and *Zamia* of scalariform tracheids. According to Sifton (1920, 1922) and Bailey (1925) the alternate and opposite pitting is directly developed from scalariform types. As regards the general course and organization of the leaf traces in the cortex, *Dioon* was studied by Langdon (1920) and others. Of the several strands separating from the vascular cylinder for each leaf, the two inner pursue a vertical course into the petiole, while the remaining traces pass obliquely upwards into the cortex and the leaf base, where they anastomose and form two girdles. Girdling is characteristic of most cycads, but in the adult stem of *Macrozamia* and in the seedling of *Bowenia* the trace bundles take a direct course—a more primitive condition. The structure of the cycadean foliar bundle and its significance in phylogenetic connections also attracted attention. Two opinions opposed one another. One (Scott, 1923) was that this bundle is strictly mesarch and agrees closely with that of *Lyginopteris*. Other anatomists (Chauvead, 1912) instead designated the cycadean foliar bundle as diploxylic on the ground that the centrifugal and centripetal xylem were of independent origin and remained distinct during most of their course along the petiole.

The formation of a large number of spermatozoids in *Microcycas* aroused great interest from the taxonomic viewpoint. Reynolds (1924) stated that this genus has both primitive and advanced characters; that most of the former appear in the gametophytic generation, while most of the latter are in the sporophytic generation; and that, since the advanced characters are more numerous than the primitive, *Microcycas* should be regarded as one of the more advanced cycads.

Worsdell (1906) regarded the cycadean stele as derived from that of the polystelic Medullosaceae. Scott (1923 and earlier), on the other hand, would have the cycadean type of vascular anatomy derived from that characterizing the Lyginopteridaceae. Matte (1904) believed that the cycads originated from the latter through the Medullosaceae. In her study of *Sutcliffia*, de Fraine (1912) agreed with Worsdell that their probable origin was along the medullosean line, but from monostelic (and protostelic) rather than from polystelic forms. From the available evidence it seemed to Bancroft (1914) safe to presume that both pteridosperm families had arisen from a basal stock which also had originated the cycadean line. The cycads were generally regarded as being related to the mesozoic bennettites. Wieland (1906, 1916) retained both groups in the Cycadales, notwithstanding great differences in the morphology of the reproductive organs, but this view was later abandoned.

Bennettitales

Very important progress was made in the study of the bennettites, primarily by the epoch-making work of Wieland (1906, 1916). It gradually became evident that the great majority of cycadlike plants of mesozoic age belonged to this group. Nathorst (1902) proposed the name Cycadophyta as a noncommittal designation of all cycadlike gymnosperms. Two main groups of bennettites were distinguished, the Williamsoniaceae, of a higher average geological age, and the Bennettitaceae (Cycadeoidaceae). These groups agree closely in the structure of their reproductive organs, but differ in vegetative features. While the former had slender, often branched stems, the latter were characterized by short, stout trunks, and their strobili or flowers were embedded in a thick mantle of persistent leaf bases and ramenta.

Williamsonia has short, stalked, probably unisexual fertile shoots covered with spirally arranged scale leaves. Seward (1912) found the conical upper part of the axis densely covered by both stalked ovules and interseminal scales. Nathorst (1909, 1911, 1912) was the first to discover the male flowers of *Williamsonia*. These consist of a whorl of leaflike microsporophylls fused in their lower parts and placed on a short peduncle. The microsporophylls are either pinnate or simple, and bear synangia. *Williamsoniella* (Thomas, 1915) has instead bisexual flowers. Each consists of a whorl of microsporophylls bearing synangia, and inside them a central column extending upwards into a sterile summit, but for the greater part covered with sessile ovules and interseminal scales. *Wielandiella* (Nathorst, 1902, 1909) has branched stems like *Williamsoniella,* but its flowers are sessile instead of pedunculate. The microsporophylls were probably simple; the gynoeceum agreed with conditions in *Williamsonia.*

The stems of *Cycadeoidea* (Wieland, l.c.) resemble in their external features those of the living cycads, and their leaves are pinnately compound, but the leaf traces are simple and of a less complicated course. The flowers are bisexual and borne terminally on short axillary shoots, covered with spirally arranged pinnate bracts. The microsporophylls are whorled and form a disc by fusion of their bases. They are pinnately compound and exhibit two rows of complex synangia on each pinna. Just above the microsporophylls the apex of the fertile shoot forms a broadly cone-shaped receptacle which bears stalked, orthotropous ovules and interseminal scales. The tips of the latter are fused between the ovules to form a continuous surface layer.

In the cycadeoideas the scalariform-pitted tracheids dominate the centrifugal xylem, but are sometimes succeeded by tracheids with bordered pits. The structure of the stomata in the bennettites (Thomas and Bancroft, 1913; Thomas 1930) is quite distinct from that of the cycads.

Wieland (1906, 1916, 1919) regarded the true cycads and the bennettites as having in late paleozoic time separated from a common hypothetic pteridosperm ancestor. Scott (1923) stated, however, that there is no clue to the origin of the Bennettitales beyond the general pteridospermous hypothesis.

Cordaitales

Advances in this group relate less to the reproductive than to the vegetative organs. C. E. Bertrand's (1911) interpretation of the morphology of their female flowers differs only slightly from that of Renault (1879). Schoute (1925) found, however, that the inflorescence is simple, and each fertile "bud" on the main uniaxial. The flower axis carries scales and megasporophylls arranged in a spiral. *Mesoxylon* (Scott, 1923; Maslen, 1930) is anatomically intermediate between *Poroxylon* and *Cordaites.* The wide pith is discoid; the wood is made up of tracheids with multiseriate bordered pits, and has uniseriate rays. In contrast to *Cordaites,* centripetal wood forms parts of the double leaf traces at the margin of the pith. Other types of paleozoic stems allied to the cordaites also became known. The genus *Callixylon* (Arnold, 1930), otherwise highly differentiated, has mesarch primary wood. Cordaitean wood has a wide region of transition between the spiral elements of the protoxylem and the first pitted elements of the secondary wood (Penhallow, 1907; Bailey, 1925). The sequence of structural changes exhibits recapitulation of successive evolutionary modifications of the derivation of multiseriate bordered pitting from scalariform pitting. The roots and rootlets (Halket, 1930) were found to resemble those of present-day gymnosperms. Leclercq (1928) and earlier authors showed that cordaitalean leaves were rather variable in structure. Coulter and Chamberlain (1917) and Scott (1923) believed that the Cordaitales and pteridosperms had a common origin, while Chamberlain (1920), Sahni (1920), etc., regarded them as belonging to two distinct evolutionary lines.

Ginkgoales

Sprecher (1907) described in detail all the organs of *Ginkgo.* The female flower was continuously debated (Haan, 1920). Sprecher, Coulter and Chamberlain (1917), Goebel (1923), Pilger (1926), and Sakisaka (1929) looked upon the collar as a reduced megasporophyll bearing an ovule terminally, while Zimmermann (1930) characterized the flower in the terms of his telome theory as a dichotomized truss with terminal megasporangia. Similarly the primitive male organ of *Ginkgo* was, in Doyle's (1926) opinion, not a flattened leaf, but a sporangiophoric structure carrying terminal microsporangia. According to Goebel, *Ginkgo* differs from other gymnosperms by having an endothecium in the microsporangium. Jeffrey and Torrey (1916) distinguished two types of microsporangiate opening mechanism, an ectokinetic, characteristic of lower vascular plants, and an endokinetic. The latter occurs in a fiber layer derived from the fibrovascular tissues, and is said to be present characteristically in living seed plants (except the cycads). Jeffrey (1917) further pointed out that nearest to the primary wood in the xylem of the peduncle the transition region shows tracheids without rims of Sanio (crassulae), and the bordered pitting is largely alternate, while opposite pitting and rims, characteristic of the mature secondary wood, are developed farther away. These conditions were believed to indicate the derivation of the Ginkgoales from cordaitalean ancestry. In the stem wood the transitional inner portion is narrower than in more primitive gymnosperms (Bailey, 1925), and the circular type of bordered pitting tends to work back into the protoxylem, so that typical scalariform and transitional types are almost completely eliminated. Coulter and Chamberlain (1917) held that the Ginkgoales were either derived from the Cordaitales, as Jeffrey believed, or the two groups had become differentiated from some common stock of paleozoic age, which was Scott's (1923) opinion.

Coniferae

As regards the interpretation of the female organs of the conifers there were at the outset four main rivaling theories: (1) the excrescence theory of Sachs-Eichler; (2) the foliolar theory of Delpino and Penzig; (3) the brachyblast theory of Braun and Čelakovský; and (4) van Tieghem's modification of the last-mentioned theory. Pilger's summary (1926) shows that opinions remained divergent. The excrescence theory was supported by Pilger himself and by many others. Penzig (1922) maintained the foliolar theory, while Jeffrey (1917), Eames (1913), Sinnott (1913), Aase (1915), Sahni (1920), Walton (1928), and Zimmermann (1930) professed the brachyblast theory. Wettstein (1911) and Herzfeld (1914) also regarded the female cone as an inflorescence, but the flower was said to consist of a strongly reduced axis axillary to the bract, and of one or more megasporophylls, almost completely used up in the formation of the terminal ovules. Secondary outgrowths from the floral axis, more or less fused reciprocally and with the bract, form the ovuliferous scale. Goebel (1923) agreed closely with Wettstein, but regarded the ovuliferous scale as made up of outgrowths from the megasporophylls. The conifers (including the taxads) were commonly regarded as a monophyletic group, and their female cones were interpreted either as inflorescences or as flowers. However, Lotsy (1911) divided them into the Florales (Podocarpaceae, Araucariaceae, and Cupressaceae) and the Inflorescentiales (Taxaceae, Taxodiaceae, and Pinaceae), and Thomson (1909) distinguished one aplosporophyllous group (Podocarpaceae and Araucariaceae) and another diplosporophyllous group (Pinaceae, Taxodiaceae, and Cupressaceae). If both simple and compound strobili really occurred in the conifers, this would seriously affect the unity of the group. But Eames and Aase showed that the female flowers of the Pinaceae and Araucariaceae are homologous. Eames found that the Araucariaceae, Taxodiaceae, and Podocarpaceae exhibit complete transitions—even within themselves—by fusion and reduction from forms with distinctly compound strobilar units to other, apparently simple forms. Mitra's (1927) discovery of the occurrence of biovulate cone scales in *Araucaria* suggests that the uniovulate condition is an advanced rather than a primitive feature, and that both types may be derived from a triovulate type.

According to Dupler (1920), who dealt with the ovuliferous shoot system of *Taxus,* its primary shoot is a persistent vegetative branch, usually of finite growth, bearing only reproductive (secondary) shoots and functioning for several successive seasons. The terminal ovule is a truly cauline structure. Its aril had been regarded as a special outgrowth, as a carpel, as an ovuliferous scale, as outer integument, and as the outer fleshy layer of a single integument. Dupler interpreted it as the fleshy layer of a three-layered seed coat, delayed in appearance. Sahni (1920) proposed the institution of a separate group, the Taxales (including *Cephalotaxus*), equal in rank to the Coniferae. As to the *Torreya* ovule, Oliver (1902, 1903) distinguished between the original ovule and a phylogenetically younger intercalated portion by introducing the terms archisperm and hyposperm to designate the respective regions.

Turning now to the male flowers, one view considered as primitive a more or less radially symmetrical microsporophyll, carrying many sporangia distally, while the other regarded the microsporophyll of the Pinaceae, with two sporangia on the dorsal surface, as the basic type. Dupler (1919) held that the peltate, perisporangiate microsporophyll had probably been carried forward to modern gymnosperms by the cordaitalean line. The araucarian microsporophylls suggest a basic peltate structure, and true peltate forms occur in *Taxus* and *Torreya* (Coulter and Land, 1905), though in the latter genus the adult sporophyll becomes hyposporangiate. Doyle (1926) believed that the primitive peltate sporophylls were never by nature foliar, but sporangiophoric. Pilger (1926, 1929), on the other hand, comprehended the microsporophyll as a metamorphosed leaf, and regarded as primitive such conifer sporophylls as only differed slightly from ordinary leaves. The microsporophyll of *Taxus*, however, was assumed to be characterized by a morphogenesis of its own.

Stimulated by the European activities in fossil botany, the wood anatomy of the gymnosperms developed into an important subject. Diverse opinions on the phylogenetic meaning of many observed structures developed, however, and conifer anatomy became a ground of debates of the first order. The type of tracheary pitting in secondary xylem was held to be of phylogenetic interest. Gothan (1905) considered that the most primitive type of bordered pitting was hexagonal, alternate, and crowding the whole tracheid wall (araucarian pitting). Elimination resulted first in small isolated groups of bordered pits, then in the uniseriate flattened condition, and finally in the scattered arrangement, where the pits occur singly or in opposite arrangement on the radial wall (modern pitting). The transitions between the two types found in fossil woods of mesozoic age were believed by Gothan to represent relatively primitive extinct Pinaceae. The Araucariaceae were the most ancient conifers, and derived from the cordaites. Jeffrey (1912), on the other hand, looked upon the araucarian wood as more recently acquired, and based this conclusion on the structure of the first annual ring of mesozoic *Araucarioxylon* stems, of the seedling of living araucarians, and especially of the wood of their cone axes. He regarded the Pinaceae as the ancient and primitive conifer group, most closely associated with the cordaites, and the Araucariaceae as derived from it. Thomson (1913) emphasized the resemblances of the Araucariaceae to the Cordaitales in the pitting of the secondary tracheids in the root and in the axis of the female cone. Jeffrey considered that the presence of rims of Sanio in the secondary tracheids adjacent to the primary wood of the cone axis in *Araucaria* and *Agathis* supported his view of the pinaceous ancestry of the araucarians. But Thomson interpreted the rimlike thickenings and alternate pitting sometimes found in the cone axis and first annual ring of stems and roots in the pines as indicating the opposite. In Bailey's (1919; cf. Pool, 1929) view, it is in both cases a question of a transitional type of tracheary pitting and not true crassulae. Sifton (1920) agreed with Bailey's statement that neither of the two argumentations is tenable. The taxonomic importance of the crassulae was very differently evaluated. Jeffrey (1912), and his associates, accepted them as an infallible criterion for diagnosing coniferous woods, while Gothan (in Potonié and Gothan, 1921) considered that Jeffrey's school exaggerated their importance. Bailey (1925) asserted that the conifers are, in contradistinction to the cordaites, characterized by the circular bordered pits having worked back into the earlier formed portions of the primary xylem, and by the elimination from the transitional zone of the stele of typical scalariform and transitional types of bordered pitting. He found that there is nothing to indicate whether opposite pitting is derived from alternate or *vice versa,* or whether both types were independently originated.

Gothan (1905) proved the value of the ray-cell structure to the classification of coniferous woods. His abietinean pitting is characterized by strongly pitted horizontal and vertical ray-cell walls and circular pits. He discerned several types of tracheary pits visible through the crossing fields of the ray cells. The normal occurrence of ray tracheids in the Pinaceae is according to him an advanced feature. Penhallow (1907) believed marginal ray tracheids to be derived from parenchyma cells, while Thompson (1910) interpreted them as modified tracheids. In Penhallow's opinion the rare occurrences of ray tracheids in certain conifers constitute the first evidence of a tendancy in development which was only fully realized at a later period, but Jeffrey (1917, 1925) and others, read the series in the opposite direction, interpreting this feature as vestigial or reversionary, and indicating pinaceous ancestry. Great importance was also attached to the occurrence and distribution of resin cells and canals in the conifers. Penhallow held that scattered resin cells indicate a primitive condition, and that their aggregation into groups containing resin canals, as in the pines, is an advanced feature. At the end of the period under review, the general opinion was still that the Pinaceae, with a well-developed system of resin canals, were highest on the scale of conifers (Thomson and Sifton, 1925), but Jeffrey considered their presence a primitive condition. The Taxodiaceae and Cupressaceae, as well as the Araucariaceae, are, according to him, mesozoic offshoots of the Pinaceae, of which *Pinus* would be the most ancient and primitive genus, directly derived from the cordaites.

Jeffrey (1908) considered, moreover, leaf anatomy to be of phylogenetic significance, and tried in that way to gain further support for his views. One argument was the occurrence in the Pinaceae of vestiges of double leaf-traces, but in 1904 Chauveaud had shown that the doubling of the foliar bundle in *Abies* and *Pinus* is a result of secondary modifications. Further arguments were: (1) the presence of true centripetal wood in the genus *Prepinus* of cretaceous age, believed to be a progenitor of *Pinus;* (2) the resemblance of the foliar bundle of *Prepinus* to that of certain cordaites in the presence of centripetal wood and a double sheath of transfusion tissue; and (3) the persistence of the double transfusionary sheath in the true pines of the cretaceous. *Prepinus* had deciduous short shoots of a generalized type bearing numerous spirally arranged leaves, in contradistinction to a few whorled fascicular leaves of the highly specialized living pines. The short shoot was a primitive attribute of the coniferous stock. Thomson (1914), on the other hand, argued that in the pines the short shoot is a specialized branch of finite growth with a determinate number of leaves, whereas its progenitor apparently was an ordinary branch, and that therefore the short shoot could not be considered an indicator of primitiveness.

Burlingame (1915b) discerned three principal theories of the origin of the conifers and their relationships. According to the *"lycopod"* theory, which still had a few adherents in the 1920's, the female conifer cone was a flower, and the cone scale a sporophyll differentiated into a spore-bearing and a foliar part. The Pinaceae were consequently more specialized forms than most other conifers. The "cordaitean" theory was adopted by the majority of students. The arguments advanced in support of it included: the resemblances between the cordaites and the araucarians in the anatomy of the stem, root, and leaf; the difficulty in explaining the cones of the Pinaceae in terms of a lycopod ancestry; the structure of the seed; the multiple microsporangia. The Araucariaceae were regarded as the primitive basal group of conifers, or as constituting an independent evolutionary line. The "abietinean" theory, advanced by Jeffrey (1912) is based on the brachyblast theory of the female cone, and on certain principles of comparative morphology. He argued in the following way:

1. The ancestors of *Araucaria* and *Agathis* cannot be derived from the cordaites because they had wood parenchyma and strongly pitted rays in their secondary wood. Certain mesozoic woods with araucarian pitting, wood parenchyma, and strongly pitted rays, are of araucarian affinity; their characteristic features are retained in the wood of the cone axis, root, and first annual ring of vigorous branches of living Araucariaceae.
2. The structure of the first annual ring of mesozoic *Araucarioxylon* stems, as well as of the seedling wood in the cone axes of *Agathis* and *Araucaria*, shows that the araucarian tracheary pitting is not ancestral, but more recently acquired.
3. Certain mesozoic conifer woods with traumatic resin canals are of araucarian affinities, since their tracheids have araucarian pitting, and there are no crassulae. Abietineous pitting in the rays of extinct conifers is no reliable diagnostic feature. Traumatic phenomena supply an additional argument in favor of the derivation of the Araucariaceae from pinaceous ancestry.
4. The Araucariaceae cannot be derived from the cordaites, since they possessed primitively a number of features which never existed in the cordaitean stock. The *Araucarioxylon* type is derived from ancestral forms possessing opposite pitting, crassulae, strongly pitted rays, and horizontal and vertical resin canals.

In contrast to Jeffrey's theory, Gothan (in H. Potonié and Gothan, 1921), Kräusel (1919), Eckhold (1922), and others, regarded the Araucariaceae as the most primitive and the Pinaceae as the most advanced conifers. The appearance of a transitional group, the Protopinaceae, in the Mesozoic era was combined with a reduced frequency of araucarian woods and the gradual appearance of pinaceous woods. The pitting of the tracheids changed concurrently with other features, e.g., the form and arrangement of the cross-field pits, the occurrence of vertical and horizontal resin canals, and of ray tracheids. A phylogenetic line could thus be followed from the simple woods of araucarian structure, via the Protopinaceae and their nearest successors, to the modern pinaceous wood of complex structure.

That opinions on the relationships of other families also differed was to some extent due to these contrasting general views. The taxads, *Cephalotaxus*, podocarps, and their allies, were at the beginning of the century still regarded as members of one family, Taxaceae, but gradually it was realized that this was a diverse assemblage, which should be divided into no less than three families, viz., the Podocarpaceae, Cephalotaxaceae, and Taxaceae s. str. (Pilger, 1926). Sahni (1920) even excluded the genera *Taxus, Torreya,* and *Cephalotaxus* from the conifers, and proposed for them an independent phylum, Taxales, related to *Ginkgo,* to the Cordaitales, and to the Coniferae. According to Sahni the Taxales stand apart from the conifers in the general organization of their female shoots, and in the fact that they retain primitive seed and seedling characters. He did not believe that the yews represented any relatively modern group, as asserted by Jeffrey.

Numerous contributions were made to our knowledge of the conifers of past geological ages, their external morphology, anatomy, and taxonomy. Hollick and Jeffrey (1909), Stopes and Fujii (1910), and Ogura (1930–1932) dealt with the anatomy of various conifers of cretaceous age. Nathorst (1908) worked out the morphology of the female cones of the early mesozoic genera *Palissya* and *Stachyotaxus,* and Schlüter and Schmidt (1927) observed the double cone scale of a triassic *Voltzia.* Wood anatomy as applied to fossil material also attracted attention. A critical review of this subject was published by Kräusel (1919).

Gnetales (Chlamydospermae)

Solms-Laubach (1908) thought that the three genera of the Gnetaceae had nothing in common, except that they were neither conifers nor cycads.

Ephedraceae. According to Thoday and Berridge (1912) a reduction can be traced in the microsporangiate shoot, from clearly bifid sporangiophores with four bilocular synangia to each half, to nonbifid sporangiophores on which increasing numbers of sporangia are fused, often forming in the process trilocular or even quadrilocular synangia. The bipartite sporangiophore with its paired bilocular snyangia appeared to them to be homologous to the bipinnate microsporophyll of *Cycadeoidea.* Coulter and Chamberlain (1917), however, considered it an axial structure. In Pearson's (1929) opinion the male flower is a greatly reduced strobilus consisting of an axis bearing two pairs of appendages and the sporangiophore itself. The female flower was regarded as a specialized bud, generally axillary, but sometimes terminal in position. The vascular anatomy of the vegetative organs was investigated by Thompson (1912) and Jeffrey (1917). Diffuse and abundant parenchyma, vessels, and large rays, are characteristic features of the secondary wood. The tracheary pitting is similar to that of the conifers. The vessels are composed of tracheidlike segments, which have bordered pits in their radial walls, crassulae, tertiary spirals, and trabeculae. Perforations are formed on the oblique end walls by the initial enlargement of the bordered pits, by the subsequent loss of both torus and border, and often by the fusion of such contiguous perforations. Bailey (1925) stated that the primary xylem is of a highly modified type, and that there is no accurate record of successive structural changes in the evolution of the circular bordered pit in the inner zone of transitional tracheids.

Welwitschiaceae. The male (pseudohermaphrodite) flower was generally regarded as approaching most closely the primitive floral organization of the Gnetales, from which both the male and the female flowers may be derived (Pearson, 1929). The opinions of the homologies of the various parts of these were summarized by Lignier and Tison (1912). Church (1914) believed that the flowers were originally hermaphrodite, and that the functional ovulate flower represents an advanced stage of reduction. Sykes (1910a, 1910b), Lignier and Tison, and Church, contributed to the unraveling of the vascular anatomy of the flowers and ovules. The structure of the inflorescence axes is extremely complex, the bundles being arranged in two more or less definite series, and recalling to some extent, like the structure of the adult stem, the vascular anatomy of the Medullosaceae.

Gnetaceae. According to Pearson (1929) the difficulty of interpreting the inflorescences is due to peculiarities in the position and organization of the flowers. It was generally held that the two inner of the ovular envelopes were integuments, and that the outermost was a perianth. Quisumbing (1925) interpreted the outer integument as derived from the inner by differentiation of a common primordium. Lignier and Tison (1913) asserted, however, that the innermost envelope is a true ovary, and that the outer two form a perianth. In Pearson's opinion, the two outer envelopes of the complete, the single outer envelope of the incomplete, female flower are homologous with the cupule of the spike. The innermost envelope is not related to the ovary of the angiosperms. The spike and the female flower are modifications of the same primitive structure, which might have consisted of a terminal nucellus surrounded by a single ovular envelope, a ring of lateral male flowers, below which stood one or more modified leaf-pairs. Thompson (1918) demonstrated that the vessel, with a single large performation in its end wall, is evolved by the enlargement and fusion of several bordered pits, while the angiospermous vessel originates from the type with many long and narrow scalariform perforations.

The position of the Gnetales remained almost as obscure as it was at the beginning of the twentieth century. They were regarded as derived from primitive conifers by some authors, from the bennettites by others. Their supposed angiosperm characters were sometimes strongly emphasized, but the majority of botanists retained the Gnetales as an advanced and aberrant group of the gymnosperms, and considered its three recent genera to represent divergent evolutionary lines of some unknown ancestry.

Classification of the Gymnosperms

The gymnosperm systems published in the period under review reflect the differences of opinions on the affinities of certain groups. One type of scheme corresponds to the system of Engler (1892), in which the gymnosperms were divided into several equivalent classes (Wettstein, 1924; Engler and Gilg, 1924; Pilger, 1926; Zimmermann, 1930, etc.). Wettstein excluded the pteridosperms, and Zimmermann combined the Cycadales and Bennettitales in the class Cycadophyta. The other type of system is characterized by the classes being united into taxa of higher rank. Jeffrey (1917), and after him Conard (1919), divided the gymnosperms into Archigymnospermae and Metagymnospermae (Coniferales, Gnetales). Berry (1917, 1920) substituted for the Gymnospermae three groups of equivalent rank, viz., Pteridospermophyta, Cycadophyta, and Coniferophyta. Chamberlain (1920) proceeded on similar lines, but referred the pteridosperms to the Cycadophyta. Sahni (1920) distinguished between the megaphyllous Phyllospermae with leaf-borne seeds (pteridosperms and cycads), and the microphyllous Stachyspermae with stem-borne seeds (cordaites, ginkgoes, taxads, and conifers), but left the classification of the Bennettitales and Gnetales open. Van Tieghem and Costantin (1918) and Chodat (1920), finally adopted a partly different terminology. The former divided the gymnosperms into four classes, viz., (1) Pteridospermae, (2) Natrices (Cycadineae, Ginkgoineae), (3) Vectrices, and (4) Saccovuleae; while Chodat made the Saccovuleae (= chlamydosperms) into a higher unit equivalent to the gymnosperms. Berry designated Gymnospermae a taxonomic term that had outlived its usefulness for other than descriptive purposes, while Hutchinson (1924) discarded the term Coniferae. Berry held that the conifers comprised three main groups, viz., Coniferales, Araucariales, and Taxales, all ranking equally with the Ginkgoales and Cordaitales. Van Tieghem and Costantin subdivided the Vectrices into the orders Taxineae, Cupressineae, and Abietineae, but these do not correspond to Berry's units. Two orders were more frequently discerned in the Coniferae, and usually named Taxoideae (Taxales) and Pinoideae (Pinales). The division of the conifers by Lotsy (1911) into Florales and Inflorescentiales (cf. above) takes a special position. The remaining systems merely divided the conifers into families. The greatest contrasts in this respect were between the system of Engler and Gilg with two families, Taxaceae and Pinaceae, on the one hand, and on the other, those of Pilger with seven families (Taxaceae s. str., Podocarpaceae, Araucariaceae, Cephalotaxaceae, Pinaceae s. str., Taxodiaceae, and Cupressaceae) and Seward's (1919) with nine (Araucarineae, Cupressineae, Callitrineae, Sequoiineae, Sciadopitineae, Abietineae, Podocarpineae, Phyllocladineae, and Taxineae). Most students still referred the three genera of the Gnetales to one family only—Gnetaceae—but Markgraf (1926) subdivided them into three families, one for each genus, and Van Tieghem and Costantin into two orders, viz., the Ephedrineae, comprising the Tumboaceae (*Welwitschia*) and Ephedraceae, and the Gnetineae, with the Gnetaceae.

The Modern Period (from 1930)

While the rise of genetics has tended to draw attention from taxonomy and to reduce its prestige, recent developments indicate a trend towards a synthesis of the phylogenetical and the causal approaches to evolutionary problems (Mayr, 1949; and others). The mechanism of the evolution of the higher categories was regarded by Stebbins (1950) as a continuation of the processes giving rise to subspecies and species, and the origin of the former as largely a matter of time, and of further genetic and environmental changes.

Gaussen (1944–1952; cf. Ferré, 1952) formulated the following "evolutionary laws":

1. The most recent species of a phylum are generally more evolved in all characters than their ancestors.
2. When a character evolves in a definite direction, this is always maintained, and there is never a return to a more primitive type (seemingly, a return to an ancestral type may ensue on overevolution).
3. In a phylum the species generally increase in size in the course of evolution (although overevolution may lead to an apparent return to ancestral conditions).
4. Evolution proceeds towards specialization of organs and decrease in their number, as well as towards reduction in the size of certain of them, which tend to disappear; when organs have become simple, they may fuse into a complicated structure, which is then in its turn simplified.
5. The great plant groups replace one another in the course of geological times, each having a juvenile or primitive phase, a mature or evolved phase, and an old or overevolved phase.

In respect to evolutional juvenility, Gaussen distinguished three cases (cf. Ferré, 1952),

1. When a species is at the beginning of the evolution of the phylum, its juvenile forms indicate the future evolutionary trend in that phylum; the juvenile form is evolved, the adult primitive.

2. When species represent an evolved stage of the phylum, their juvenile forms are simply intermediate between the embryos and the adult forms; these species are evolved both in the juvenile and the adult phase.

3. When a species represents an overevolved stage of the phylum, its juvenile forms are evolved, and its adult forms overevolved; here the adult form is more evolved than the juvenile, however, and presents, before the juvenile form, indications of a return towards the ancestral form. Senile forms sometimes appear at the end of the evolution of a phylum.

The type of evolution characterized by an apparent return to primitive conditions is called pseudocyclic (Gaussen, 1952).

The nature of the alternation of generations remained a matter of controversy. Bower (1929, 1935) retained the same general attitude as in 1908, although modifying it in the light of later work. He thus restated his antithetic theory, now called the theory of interpolation, and contrasted it with the homologous or transformation theory. Zimmermann (1949) emphasized that the arguments against Bower's theory did not disprove the view that the divergent differentiation of the two alternating generations is an adaptation to life on land. In later years problems of this kind have been discussed mainly from the genetic point of view.

The organization of the sporophyte body of vascular plants in general, and the "telome" theory (Zimmermann, 1930, 1949, 1952; cf. Halle, 1933; Bower, 1935; Eames, 1936; Lamm, 1948, 1952; Stebbins, 1950; Florin, 1951) in particular, attracted great attention. This is a phylogenetic theory proceeding from the structure of known primordial plants, and combining results of research on external form, internal structure (stelar theory), and ontogenetic development (alternation of generations). Its main points are as follows:

1. The vascular land plants originated from seaweeds with dichotomously branching thallus. Primitive telomes ("Urtelome") derive from unicellular stages by combination of cells, formation of meristem (origin of polarity), rotation of cell axis, shifting of main phases in alternation of generations, and formation of various permanent tissues.

2. The first vascular plants were composed of undifferentiated uniform organs, or telomes in a wide sense. Such telomes comprise telomes in a restricted sense—the ultimate uninerved segments of a dichotomizing branch system—and mesomes, which are similar segments between subsequent points of forking. Both were protostelic. The telomes were divided into vegetative telomes or phylloids, and fertile telomes or terminal sporangia, producing spores.

3. The evolution of the vascular plants in all subsequent geological periods is the result of a few basic morphological trends: overtopping, planation, syngenesis or fusion, reduction, recurvation, and longitudinal differentiation.

The shoot of seed-plants was studied by Bower (1930) from the point of view of the relation between size and form. Various aspects of the relationships between stem and leaf have been subjected to study. Arber (1950) regarded the leaf as a partial shoot borne by a whole shoot, and with an urge towards self-completion as a whole shoot. The phytonic theory of the phyllorhize, involving a root attendant on each leaf, was discussed by Boureau (1939, 1952) on the basis of ontogenetic investigations of the anatomy of seedlings in the Pinaceae and other conifers. Bower (1935), Eames (1936), and Emberger (1952a), however, considered the phytonic theories valueless. The evidence of the organization of primary shoots was characterized by Wetmore (1943) as still too incomplete to permit of generalizations. Barthelmess (1935) and Esau (1943) considered the primary vascular system to be made up only of leaf traces forming sympodia. Barthelmess studied the relations between phyllotaxis and stelar structure, and supported the idea of the most equitable spatial arrangement being at the growing apex. He believed that the leaf traces differentiate basipetally towards preformed parenchymatous gaps in the primary meristem ring. Sterling (1945) recapitulated the main views expressed in order to explain the regularity of leaf arrangement. One of these is based on the concept of the genetic spiral, and another considers the genetic spiral a secondary phenomenon resulting from the influence of the contact parastichies. He suggested a third interpretation, according to which the arrangement of foliar members at the shoot apex is also to some extent determined by the vascular structure of the shoot. The procambial strands were found to differentiate acropetally in the shoot apex of *Sequoia* from older strands below. There are no cauline bundles; the bundles are common to both stem and leaf. According to Gunckel and Wetmore (1946) the two procambial strands of a *Ginkgo* leaf develop continuously and acropetally from definite procambial strands already present in the lower axis. Finally, Plantefol (1948) presented a theory of the multiple foliar helices, which he considered applicable to the phyllotactic patterns of all cormophytes.

In respect to the nature of the various types of leaves in gymnosperms Florin (1938–1945) arrived at the opinion that megaphylls and microphylls are not fundamentally different. Both categories of leaves appear to originate from radial dichotomized telome systems, which, however, differed in size and complexity, and in their subsequent development. In the majority of conifers the uninerved leaves appear to have been formed by direct reduction of little complicated, cruciately dichotomized telome systems without either planation, fusion or telones, or aggregation. According to Němejc (1950) the cycadophytes have megaphylous leaves, while the leaves of the coniferophytes are of the sphenopsid type, i.e., they are transformed short lateral branches.

The interest in the fundamental structure and evolution of shoot apices was revived, and directed not least to the gymnosperms. In his review in 1939 of our then rather meager knowledge of this subject, Foster recalled that neither the apical cell theory nor the histogen theory had proved a satisfactory interpretation of the shoot apex in gymnosperms. The latter theory had been superseded by the tunica-corpus concept, first stated by Schmidt (1924). In 1941 Foster reported the main results of studies of this kind in the preceding five years. The cells of the "primordial meristem" were segregated into more or less well-defined tissue zones reflecting the type, direction, and distribution of growth. Later, Johnson (1951; cf. Popham, 1951) summed up the subject and suggested that the organization of the stem apex may be of value in tracing relationships. He pointed out that the apices of all investigated gymnosperms agree in having a superficial initiation zone, a group of subapical mother cells, and a flanking zone. Comparative studies had revealed the existence of four types of terminal meristem, viz., the cycadophyte type, the ginkgophyte type, the coniferophyte type, and the tunica-corpus type, of which the latter appears to be the most advanced, and has been attained in *Araucaria* (Griffith, 1952) and in chlamydosperms. In this connection the initiation and differentiation of gymnosperm leaves attracted attention from the point of view of the evolutionary history of the foliar types in higher vascular plants, but only a few complete accounts have yet been presented of gymnosperms. Various aspects of developmental morphology were discussed by Sifton (1944).

The results of the researches into the origin and development of primary vascular tissues in seed plants were reviewed by Esau (1943). Bailey continued his investigations of the structure of the cambium and its derivative tissues, and clarified to a considerable extent the problem of the cell wall structure of higher plants (Bailey, 1940). He suggested that the old and still open question of the mode of formation of the secondary wall—whether by intussusception or by apposition—will ultimately be solved essentially in favor of the latter alternative. Other workers interested themselves in the origin, development, and distribution of xylem rays in gymnosperms. According to Bannan (1934) the evidence of the phylogeny and of the ontogenetic sequence indicates that the primitive ray is parenchymatous, and that ray tracheids have arisen at the expense of parenchyma. Esau (1939, 1950) also summed up the work done on phloem tissue. This kind of research had come almost to a standstill about the end of the nineteenth century, and was not revived until more than thirty years later. Pith structure, particularly in conifers, had been even more neglected until Doyle and Doyle (1948) began a series of works in this field. The origin of transfusion tissue in the leaves of cycads, *Ginkgo,* and conifers was again brought up for discussion. Van Abbema (1934) held that Mohl's (1871) theory that the central transfusion tissue is nothing but modified parenchyma and thus of the same nature as the accessory transfusion tissue, was likely to be correct, while Huber (1948) supported Worsdell's theory of 1897. The marked advances of late years in our knowledge of gymnosperm anatomy have been summarized by Eames and MacDaniels (1947) and Foster (1949). The structure of the epidermis was, however, only cursorily treated. Florin (1931, 1933) studied the epidermal characters of the recent gymnosperms from the taxonomic point of view, and found that external leaf morphology and epidermal structure—with special reference to the structure of the stomatal apparatus—constitute a feature complex which is generally well suited to serve as a means of characterizing natural species groups of generic rank.

In the pteridosperms and the cycads the guard cells of the stomatal apparatus are directly originated by the primary mother cell. The surrounding (perigene) epidermal cells may function directly as subsidiary cells, or each may divide into one subsidiary and one or more radially arranged encircling cells. This primitive haplocheilic or simple-lipped type also characterizes the cordaites, ginkgophytes, conifers, taxads, and ephedras. In the bennettites, on the other hand, the primary mother cell of the guard cells usually divides into three cells, of which the median cell gives rise to the guard cells, and the two (mesogene) lateral cells function as subsidiary cells. One or both of the lateral cells may also divide into one subsidiary and one encircling cell. This is the syndetocheilic or compound-lipped type of stomata of the gymnosperms, which—apart from the bennettites—occurs only in the living genera *Welwitschia* (Florin, 1934) and *Gnetum.* The haplocheilic type of stomata in gymnosperms is primitive and the syndetocheilic type advanced. This accords with the fact that all paleozoic gymnosperms so far examined have haplocheilic stomata, while the syndetocheilic type does not appear until mesozoic time. The mode of development of the stomatal apparatus thus constitutes a character sometimes separating taxonomic groups of high rank. It has become of special importance in connection with the classification of fossil leaves of cycadlike type in deposits of mesozoic age. Also Harris (1932–1937, 1942–1952) has investigated the stomatal structures in cycads, living and extinct, as well as in bennettites, fossil ginkgophytes, and conifers, etc. The stomata of the ginkgophytes were subjected to further study from the taxonomic point of view by Florin (1936a), who, in addition, in a still later work (1938–1945, 1951) described the epidermal structures of the leaves of the oldest known conifers of paleozoic age, and compared them with those of the cordaites. Orr (1937) tested the value for diagnostic purposes of these structures in living conifers in general, and Cookson and Duigan (1951) in recent and fossal Araucariaceae.

Research devoted to the gametophytes has continued in the modern period, although with less intensity than that characterizing the first thirty years of the present century. Its aim has been to fill remaining gaps in our knowledge of their development and organization. Doak (1932) confirmed Juel's (1904) observation that in *Cupressus* the pollen tube often develops a complex of several male cells instead of the usual two, and considered this feature to be a reversion. Florin (1936b) studied the structure of the male cordaitean gametophyte at the shedding stage of the pollen grains. The central body of the grain was not filled by walled cells, as Renault (1879) had believed, but appeared possibly to have a peripheral layer of such cells. The interior of the body contained a central row of free nuclei orientated along the vertical axis of the pollen grain. No pollen tubes have so far been found in paleozoic gymnosperms. Summaries of the comparative cytology of the sexual apparatus and of the evolution of the archegonium were published by Schnarf (1941, 1942). Regarding the development of the male and female gametes, he emphasized their formation in pairs. This "Zweier-Gesetz" is always modified in the female sex, however, and sometimes also in the male, one of the two gametes having degenerated or assumed a special function. General discussions of the evolutionary trends of the gymnosperm gametophytes were given by Fagerlind (1941) and Battaglia (1951).

A pronounced feature of the period under review is that to a large extent the interest in "life-histories" of gymnosperms shifted from the development of the gametophytes and proembryo to their embryogeny as a whole. Johansen (1950) has recently summarized our knowledge of gymnosperm embryology with a view to facilitating correlation and evaluation of the results obtained. Buchholz (1933) distinguished two kinds of cleavage polyembryony in conifers, determinate and indeterminate. In determinate cleavage polyembryony one embryo is more favorably situated than the others, and ordinarily becomes the successful embryo, while in the indeterminate condition any one of several embryos derived from the same zygote may survive. According to him, the probable steps in the evolution of polyembryony were: (1) indeterminate cleavage polyembryony; (2) determinate cleavage polyembryony; (3) simple polyembryony showing definite faces of determinate cleavage polyembryony; and (4) simple polyembryony without any such traces. The phylogenetic theories developed in conifer embryogeny by Buchholz have not been undisputed. In discussing the Podocarpaceae, Doyle and Looby (1939) stated that the simple embryogeny of *Stachycarpus, Saxegothaea,* and *Phyllocladus* appeared to be basal in the family, and that two different types of polyembryony had derived from it. Allen (1946b) found the relation of simple to cleavage polyembryony still obscure, and suggested that the former might represent a less specialized condition than the latter. According to Thomson (1945), Buchholz's explanation is essentially a defense of the primitiveness of the embryogeny of *Pinus* and of the phylogenetic significance attached to this genus by Jeffrey (1917). The relative frequencies of simple and cleavage polyembryony in lower and higher gymnosperm groups indicate that the simple type is primitive and has been replaced by the cleavage type. Sufficient proof that simple embryogeny in conifers differs in origin and character from that in other plants has not been produced. Cleavage polyembryony might, moreover, have originated independently in various families, and may thus be of less phylogenetic value than has generally been supposed.

Interest in palynology in general was strongly promoted at the beginning of the modern period, chiefly by the appearance of a manual by Wodehouse (1935). He discussed the principles involved in the study of pollen grains, furnished a method of approach, described the grain forms of various families, and discussed evolutionary tendencies and relationships within and between the groups. His treatment of the morphology of the grains in lower gymnosperms was incomplete and misleading, however.

The microspores of pteridosperms were studied by Halle (1933), Schopf (1948), and especially by Florin (1937), who emphasized the occurrence of two main types in this group, one of which—large, ellipsoidal grains, provided with a monolete, often somewhat deflected mark near the middle, and furrowed distally—appears to be characteristic of the Medullosaceae. Florin (1936b, 1938–1945, 1951) further investigated the microspores in paleozoic conifers. They are of the same general type as those of the cordaites, and have an annulate air sac, interrupted only at the distal pole. Upper permian conifers, on the other hand, have pollen grains with two air sacs. The former type is therefore relatively primitive in the conifers, while the grains of the living Pinaceae and Podocarpaceae—with two or three smaller sacs, or with no air sac at all—are reduced structures. R. Potonié (1952) then discussed the ontogeny, origin, and evolution of the air sacs, and Schopf, Wilson and Bentall (1944) classified microspores occurring isolated in paleozoic deposits. Müller-Stoll (1948) distinguished pinoid, laricoid, and taxoid conifer pollen in relation to wall structure and behavior at germination, and regarded as most primitive the monocolpate pollen of cycads, *Ginkgo,* bennettites, and cordaites. Palynological studies of living conifers were in particular carried out with reference to the Pinaceae, Taxodiaceae, and Podocarpaceae (Campo-Duplan, 1950, 1951; Ueno, 1951; Cranwell, 1941).

Emberger (1944 and earlier) brought up for discussion the nature of the lower gymnosperm seeds. The "seeds" of pteridosperms and cordaites, although externally resembling true seeds, are really of the nature of fertilized ovules at the shedding stage. These plants thus shed megasporangia, each enclosed in an integument, instead of true seeds containing embryos. To Emberger this meant that the lower gymnosperms were praephanerogams, with a position intermediate between vascular cryptogams and phanerogams. Favre-Duchartre (1943; cf. T.-L. Li, 1934) asserted that the seeds of *Ginkgo* behaved in a similar way. Chadefaud (1944) regarded moreover the cycads as representing the "praephanerogamous stage," Mangenot (1952) supported the conception of Emberger in contradistinction to Gaussen (1944–1952) and Lam (1948). Arnold (1948), Martens (1948), and Walton (1952) did not believe that there was any genuine difference between the seed-like ovules of paleozoic plants and the seeds of modern ones, but only a delay in embryo development until the termination of a rest period. Emberger (1949, 1952b) defended, however, the notion of praephanerogams and their position as a distinct large natural group of vascular plants. A critical analysis of the problem was then presented by Martens (1951). As regards external characters, the ovule and the seed—as well as the praephanerogams and the phanerogams—are contradistinctive, but this does generally not apply to other features. Embryo formation before shedding is a character common to conifers and bennettites, but does not apply to chlamydosperms. The contrasted feature—embryo formation after shedding—is extremely variable. The praephanerogams shed either spores or prothallia that have just been fertilized, or even embryos, while the phanerogams in some cases shed just fertilized prothallia (*Gnetum*), but nearly always embryos. The criterion of a true seed, based on the accumulation of food-reserves in the prothallium, is valid for the conifers, but not for all chlamydosperms (*Ephedra*). The character of the integument attributed by Emberger to the ovule of the "praephanerogams" is valid, but the contrasted feature is invalid in numerous conifers as a criterion of true seeds. Martens moreover pointed out the difficulties involved in classifying the bennettites with the true phanerogams, in separating the cordaites and ginkgoes from the conifers—and the cycads from the bennettites—and in putting together such widely different groups as the cordaites and the pteridosperms.

Hagerup (1933) interpreted the integument of a conifer ovule as a megasporophyll carrying the megosporangium on its ventral side. It differs distinctly from the corresponding organs of cycads and ferns, and conifers and cycads can therefore not be referred to the same higher group, the gymnosperms. Hagerup's theory was accepted by Emberger (1944, 1950), but in most other quarters it now appears to be rejected. Halle (1937) and Walton (1952) regarded the integument of pteridosperm ovules as a syntelome surrounding a fertile telome. In Florin's (1951) opinion, the integument of the ovule in cordaites and conifers is formed by collateral fusion of two uninerved branches (sterile telomes) of the megasporophyll enclosing the single terminal megasporangium (fertile telome). The megasporophyll of the conifers constitutes a telome system, producing as a rule one terminal ovule by dichotomy, overtopping, and aggregation of telomes. In the taxads, however, the integument is probably formed out of two or more sterile, aggregated telomes—or in certain cases small telome systems—which are overtopped branches of the floral axis. The position of each component corresponds to that of a megasporophyll (sporangial truss) in the cordaites and conifers. According to Eames (1952), the ovular integument of *Ephedra* is also made up of two components.

The conifer pollen grains and ovules have moreover been studied from the point of view of the evolution of pollination mechanisms. Doyle (1945) suggested that the micropyle of the erect ovule of the paleozoic *Lebachia,* which possesses more or less erect female cones, exuded a pollination fluid in which the wind-borne pollen grains were caught. The annulate air sac caused the grain to float with its distal germinal zone directed towards the nucellus. Pollination exudate still characterizes cycads, *Ginkgo,* taxads, and chlamydosperms, and occurs in all conifer families except the araucarians. The permian inversion of the ovule was combined with a reduction of the single large air sac into two separate smaller sacs, placed in such a position that the grain was brought upwards through the micropyle with the germinal zone directed as before towards the nucellus. From this stage, Doyle recognized two lines of development in the Pinaceae. The primitive flotation mechanism was suppressed in both, but in different ways. In the Araucariaceae, the grains fall on the cone scales and develop long tubes growing towards the ovule—an advanced type of mechanism, derived from the direct ovular reception type characterizing paleozoic conifers.

A significant trait of modern systematics is the combination of cytology and taxonomy into cytotaxonomy (Anderson, 1937; Sharp, 1943). It is mainly the number, morphology, and behavior of the chromosomes that are of importance. The gymnosperms are remarkable for the stability of their chromosome numbers and morphology. Lists of such numbers have been published by Sax and Sax (1933), Sax and Beal (1934), Darlington and Janaki Ammal (1945), Sugihara (1947), etc. The basic chromosome numbers of the genera in each family are as follows: Cycadaceae 8, 9, 11, 12, 13; Ginkgoaceae 12; Araucariaceae 13; Podocarpaceae 12, 13, 19, 20; Cephalotaxaceae 12; Pinaceae 11, 12, 13; Taxodiaceae 10, 11; Cupressaceae 11 (other numbers uncertain); Taxaceae 11, 12; Ephedraceae 7; Welwitschiaceae 7. The dominating numbers in the Cycadaceae are 8 and 9, in the Ginkgoaceae and Cephalotaxaceae 12, and in the Araucariaceae 13, while most conifer genera belong either to a 12 series (Pinaceae) or an 11 series (Taxodiaceae and Cupressaceae). The chlamydosperms, on the other hand, have 7 as their basic number (*Gnetum* unknown). Deviations from the primary basic numbers have been explained by Sax and Sax, and Flory (1936) as being due to the loss of one or more chromosomes following segmental interchange and polyploidy, and to fragmentation and duplication of chromosomes resulting in an increase in chromosome number. Under natural conditions polyploidy, though not of a high valence, occurs in *Picea* (Kiellander, 1950), *Pseudolarix* and *Juniperus* (Sax and Sax, 1933), *Sequoia* (Stebbins, 1948), *Ephedra* (Florin, 1932; Mehra, 1947), and *Welwitschia* (Fernandes, 1936), but after colchicine treatment of germinating seeds tetraploidy has also been brought about in *Sequoiadendron* (Jensen and Levan, 1941). The problem of the origin of the polyploids found in the conifers has recently been discussed by Andersson (1947) and Stebbins (1950).

Chemical characteristics are of value in the classification of gymnosperms, but little use has so far been made of them. A pioneer work was that of Baker and Smith (1910) on *Callitris.* Much later, Gibbs (1945) referred to the comparative chemistry of the Cupressaceae as one of the topics illustrating the use of chemistry in taxonomy. The distribution of diterpenes of the phyllocladene and podocarprene groups in the Podocarpaceae and Araucariaceae (Holloway, 1938), as well as the biochemistry of turpentines in the pines (Mirov, 1948) have been studied from the point of view of phylogenetic classification. Erdtman (1952) emphasized that constituents excreted into the dead conifer heartwood as metabolic end products should be of special taxonomic interest because of their indifference to external influences. Terpenoid constituents characterize the heartwood of the Cupressaceae in contradistinction to that of the Pinaceae.

Of interest is also the decisive difference in respect to phenolic compounds established between the subgenera *Haploxylon* and *Diploxylon* of the pines (Lindstedt, 1951). Regarding the "Königsberg genealogical tree," built up by Mez (1926) and his students on the basis of serological investigations, Molisch (1933) and Chester (1937) defended serosystematics. The latter thus believed in its having a sound basis, provided that sufficient care was taken to exclude non-specific reactions, but admitted that the whole subject was still in an imperfect stage and that further development of its techniques was needed.

Pteridospermae

Our knowledge of this group has increased considerably. Halket (1932) pointed out that even such minor characters as the structure of the root apex and the vertical orientation of the diarch xylem plate in lateral rootlets agree with modern gymnosperms rather than with ferns. Three new genera of the Lyginopteridaceae, viz., *Tetrastichia* (Gordon, 1938), *Schopfiastrum* (Andrews, 1945), and *Microspermopteris* (Baxter, 1949), were discovered. The last-named type is striking because of its small stem and leafless condition, and combines characters of both *Lyginopteris* and *Heterangium*. The evolutionary trends of stelar structure in the Medullosaceae were discussed by Schopf (1939), Baxter, Stewart (1951), and Stewart and Delevoryas (1952). A main evolutionary line and a divergent lateral branch were recognized. The former, which starts with *Sutcliffia* and continues through the permian species, has abundant stelar branching, ontogenetic and phyletic fusion, and foliar steles with conspicuous secondary tissue. The latter has transitional forms, in which little or no secondary tissue is associated with the foliar steles, and advanced species in which stelar branching is strongly reduced except for foliar steles. Contributions to the stem anatomy of the Calamopityaceae were made especially by Read (1936–1937), who described a new genus, *Diichna,* and proposed to divide the members of this family in two major groups, viz., a manoxylic, protostelic group and a pycnoxylic, medullated group. Its ancestral members were probably simple protostelic forms with but little difference between stem and leaf. The stelar histology of the pteridosperms in general was studied by Andrews (1940), who pointed out that this group can no longer be regarded as intermediate between the ferns and the cycads, and that its origin must be sought among the psilophytes, a view previously expressed by Halle (1937), Bertrand and Corsin (1938), and others. The tracheids of the secondary xylem do not appear to have ever had scalariform pitting. The characters of the primary wood are less stable than those of the secondary xylem.

Importance advances concern the polleniferous organs of the Medullosaceae. These appear to Halle (1933, 1937) to be in the main of two different types, the Potonieineae and Whittleseyineae. *Potoniea,* belonging to paripinnate *Neuropteris* fronds, is composed of stalked, cuplike, basisporangiate structures with elongate sporangia filling the whole cup. This may have been formed, phylogenetically, by collateral fusion of sterile telomes. The Whittleseyineae—comprising *Whittleseya, Aulacotheca,* and other forms—appear to be a natural group characterized by gigantic synangia borne on *Alethopteris* and imparipinnate *Neuropteris* fronds, long tubular microsporangia, and large spores of bilateral type. In *Whittleseya* they are campanulate structures, built up of a single whorl of numerous united sporangia, immersed in sterile tissue and enclosing a central cavity. *Aulacotheca,* another extreme, consists of narrow, hollow, seedlike capsules made up of whorled sporangia. Halle suggested that the synangium of this group may be derived from a terminal tuft of cyclically arranged sporangia. *Dolorotheca,* also a genus of campanulate pteridosperm male fructifications, differs from the Whittleseyineae by the tubular microsporangias not forming a single whorl. This genus was later studied by Schopf (1948; cf. Baxter, 1949), who assembled its species in the subgroup Dolerothecineae. Here, the sporangia are arranged in biseriate rows radiating from the center of the fructification. Other microsporangiate fructifications were described by Walton (1931, 1949a) and Read (1946). In *Diplopteridium* the apical, dichotomized portion of the main rachis of the frond is the synangia-bearing part. *Alcicornopteris* has tufts of free sporangia borne terminally on dichotomous branchlets. *Lacoea* (Read) consists of cupular, spore-bearing organs attached to slender rachises and believed to enclose elongate tubular sporangia on a convex receptacle.

Information on seed-bearing pteridosperm fructifications was given in some cases. The *Calathospermum* cupule was the first many-ovular type of paleozoic age in which the order and arrangements of the ovules could be studied. The presence of a crescentic bundle in its stalk suggested to Walton (1949b) that the whole structure was morphologically equivalent to an inrolled or folded frond or part of a frond. *Salpingostoma* (Gordon, 1941) is a similar many-ovular cupule. The summit of the lagenostome of their ovules is prolonged into a tubular structure called the salpinx, and there is no micropyle. In later pteridosperms, a micropyle was formed and the salpinx became strongly reduced or disappeared. Our knowledge of the anatomy of pteridosperm seeds was furthered by several writers, who dealt particularly with those of the Trigonocarpales (Hoskins and Cross, 1946, and others). Seward (1917) had classified the paleozoic seeds into the Lagenostomales, Trigonocarpales, and Cardiocarpales. The first two groups corresponded to the radiosperms of Oliver (1904), and the third to his platysperms. Loubière (1938) distinguished instead between the Nertocaryales, the Mesocaryales, and the Acrocaryales. In the first group the nucellus and integument are fused, in the second they are free except at the base; the third group is based on *Leptotesta.* But Emberger (1944; cf. Arnold 1938, 1948) disputed Loubière's interpretation of this genus, and was inclined to refer it to the Nertocaryales.

Caytoniales and Related Groups

The Caytoniaceae became much better known than they were at the end of the 1920's (Harris, 1932–1937, 1933, 1940a, 1940b, 1941b, 1951a). *Caytonia* is a pinnate megasporophyll, with the pinnae attached to a rachis and bearing ovules in rows on their incurved adaxial surfaces. The "fruit" is no carpel, and its "stigma" is not stigmatic, but merely a lip. The pollination was gymnospermous. The inner part of the "fruit" wall was thick and fleshy, embedding the seeds, and narrow canals led from the micropyles towards the lip. The microsporophyll (*Caytonanthus*) consists of a pinnately branched rachis, the lateral branches of which divide into ultimate branchlets, each bearing a quadrisporangiate synangium.

Thomas (1933) discovered a new group of mesozoic pteridospermlike plants, the Corystospermaceae, based on seed-bearing branches, male organs, and isolated seeds. The female organs (*Umkomasia,* etc.) are made up of branches partly borne in the axils of bracts and carrying terminal cupulate gymnospermous seeds characterized by curved bifid micropyles. The male organs (*Pteruchus*) show groups of terminal sessile synangia produced on cuplike or spatulate structures. The winged microspores resemble those of the Caytoniaceae. *Dicroidium, Pachypteris,* and similar types of leaves appear to belong to this family.

A third family of supposed pteridosperms of mesozoic age, the Peltaspermaceae, was instituted by Thomas (1933) and based on Harris' (1932–1937) and his own studies of *Lepidopteris,* a genus of bipinnate fronds, and its reproductive organs. The female organ (*Peltaspermum*) first described by Harris, is a peltate, cupulate "disc" with a circular series of seeds attached to its undersurface. The seed has a single integument and a curved micropylar beak. The microsporophyll (*Antevsia*) is a dichotomously branched organ bearing terminal groups of sporangia with wingless pollen grains.

Generally (Thomas, 1938; Harris; Hirmer, 1937; Andrews, 1948; and others), these families are placed tentatively in the pteridosperms and regarded as late offshoots of the paleozoic stock. They may, however, represent independent groups more or less related to one another.

Cycadales

Schuster (1932), Schnarf (1933, 1937), Chamberlain (1935), and Gaussen (1944–1952) have reviewed the cycad morphology and anatomy. Contrary to Chauveaud's opinion, Messeri (1932) and Boureau (1950) found that the centripetal wood is not a late-formed addition to the foliar bundle. According to Chrysler (1937), the pitted tracheids, together with parenchyma and rays, make up the bulk of the stem in all living genera except *Zamia* and *Stangeria,* which alone have secondary xylem consisting of scalariform tracheids. The stem wood of tuberous *Zamia* species does not exceed the scalariform stage, and represents therefore a persistent juvenile condition. Lam (1948, 1952) designated the cycads as manifestly phyllosporous in both sexes, i.e., the ovules and microsporangia are borne on many-telomed fronds or true sporophylls.

Schuster (1931) also published a list of cycads of bygone ages. Florin (1933) made this the starting-point for an investigation of the occurrence of cycads in mesozoic deposits. It turned out that a certain detached megasporophyll of early mesozoic age, *Palaeocycas,* belonged to a cycad resembling the genus *Cycas* itself. Studies of cycadlike leaves of the same age led to the recognition of a taeniopteroid type (*Bjuvia*) as the leaf of *Palaeocycas.* The plant was referred to the subfamily Cycadoideae of the Cycadaceae. Rühle von Lilienstern (1928) and Kräusel (1949a) found pinnate, bi- or pluriovulate megasporophylls of triassic age, *Dioonitocarpidium,* likewise referable to the Cycadoideae. Further, Harris (1932–1937, 1941a) proved that the genus *Beania,* comprising female cones of a type of jurassic gymnosperms bearing *Nilssonia* leaves and male cones of cycadean structure, belongs to this family and is most closely related to the subfamily Zamioideae. These discoveries indicate that true cycads already existed in early mesozoic time, but it is not yet possible to decide which of the two subfamilies is the oldest. Finally, the genera *Ctenis, Pseudoctenis,* and *Doratophyllum,* of early mesozoic age and exclusively based on leaves, their morphology, and epidermal structure, are probably true cycads.

According to Schuster (1932), the living cycad genera are end products of evolutionary lines which diverged very early. They cannot be divided into more primitive and more advanced types. Stefanoff (1936), however, adhered to the old view of the primitiveness of *Cycas,* while Gaussen (1944–1952) considered *Zamia* more primitive. It appears to be generally agreed that the cycads derive from the paleozoic pteridosperm stock.

Bennettitales

Harris (1932–1937, 1941a, 1942–1952), Florin (1933), and others, have described the epidermal structure of many types of sterile leaves, thereby furthering the classification of fossil cycadophytes. Stem anatomy was investigated by Chrysler (1932) and Wieland (1934), and the anatomy of bennettitalean roots by Carpenter (1932) and Selling (1944, 1951).

Zimmermann (1932) proved the organic connection between the hermaphrodite flower of *Williamsoniella,* the leaves of a *Nilssoniopteris,* and a certain type of stem (cf. Thomas, 1915). Harris (1944) then showed that the flower of *Williamsoniella* possessed a perianth of caducous bracts, that the free microsporophylls were pinnately branched, that the pollen was produced in two-valved capsules of the same kind as in *Cycadeoidea,* and that these two genera should be regarded as being rather closely related. Sahni (1932) discovered a new species of *Williamsonia,* the female fructifications of which were borne terminally on branches, projecting beyond the armor of leaf bases on a columnar stem with a crown of *Ptilophyllum* leaves and long scales. The female flower of *Wielandiella* was investigated by Harris (1932–1937). *Sturiella* (Kräusel, 1948) is a new type of inflorescence made up of small bisexual flowers. *Westersheimia* (Kräusel, 1949a) is unique by having pinnately branched female inflorescences, the lateral parts of which form strobili with numerous seeds and interseminal scales. Wieland (1934) investigated the bisexual flowers of *Raumeria.* Schnarf (1937) summarized our knowledge of bennettitalean and other gymnosperm seeds. Harris (1947) pointed out the need for information on the phyllotactic relations of the ovules and interseminal scales as well as their vascular connections, and on the integument of the ovule, in the cycadeoideas. The bennettitalean fructifications are sometimes called flowers, sometimes inflorescences, depending upon the supposed nature and position of the seed-bearing stalks. These are often regarded as of the nature of "leaves," but in Lam's (1952) opinion the bennettites are primarily stachyosporous in the female sex, and in that of Emberger (1944) the gynoecium is a branched axis, and the "flower" an inflorescence.

Of late years the opinion has been expressed that the pteridosperms, cycads, and bennettites form between them a natural group of high rank, the cycadophytes, the two latter divisions of which may both derive from primitive pteridosperms (Schuster, 1932; Arnold, 1948; Gaussen, 1944–1952).

Pentoxyleae. This jurassic group was described by Rao (1943), Srivastava

(1946), and especially by Sahni (1948). The branched stems (*Pentoxylon*) are polystelic; the primary bundle of each stele is surrounded by a zone of coniferlike secondary xylem. The taeniopteroid leaves (*Nipaniophyllum*) seem to have possessed syndetocheilic stomata and vascular bundles of the cycad type. The female organs (*Carnoconites*), borne terminally on branched stalks, are conelike with densely packed, sessile ovules. The Pentoxyleae combine features suggestive of the bennettites, cycads, and conifers, but the morphology of the cone and the stem anatomy indicate an isolated position. Gaussen (1944–1952), however, has tentatively referred them as a special subgroup to the Bennettitales.

Cordaitales

Frentzen (1931) investigated paleozoic woods of the form-genus *Dadoxylon*, all possessing in the radial walls of the secondary tracheids relatively small, crowded bordered pits, either primitively biseriate to multiseriate, circular to hexagonal in outline, and arranged alternately, or else uniseriate with more or less markedly flattened outline above and below (araucarian pitting). This type of wood is a feature of the Cordaitales, but it also occurs in other gymnosperms (cf. Boureau, 1949; Gaussen, 1952). Two groups are discernible: one has the radial walls of its tracheids covered by bordered pits, which the other has not. The latter appears to represent the conifer family *Lebachiaceae*. Traverse (1950) studied the primary vascular body of *Mesoxylon*. Contrary to previous opinions, the sequence of centripetal and centrifugal primary wood in the leaf traces was the same in the leaf base and in the stem. Our knowledge of the stems of the Pityeae was summarized by Arnold (1947). In a species of *Pitys*, Gordon (1935) investigated the vegetative organs anatomically. Re-examination of the whole genus served to bring *Pitys, Archaeopitys,* and *Callixylon* into close relationship, to remove them from the cordaites, and to indicate a lyginopteroid origin for the group. Cribbs (1938, 1939, 1940) discovered stems with various combinations of pityean and calamopityean features. Conclusive proof that roots of the *Amyelon* type belong to cordaites was given by Andrews (1942). Reed and Sandoe (1951) described the superficial epidermal pattern in combination with the internal anatomy of the same cordaitean leaf.

Recent investigations have materially contributed to the elucidation of the morphology of the male organs. Hirmer (1932) described the anatomy of the inflorescence axis, including the origin and course of the vascular bundles destined to innerve the strobili. Florin (1938–1945, 1951) found that the male short shoots are of the nature of strobili or "flowers." Their axes carry spirally arranged, leaflike scales, some of which are simple and sterile, while the remainder terminate in a cluster of four to six upright microsporangia. The single sporophyll bundle is bifurcated repeatedly at the apex. The microsporophyll appears to derive from a primitive radial and dichotomizing sporangial truss, the ultimate branches of which formed erect, elongate, and cylindrical sporangia. The female organs (Florin, loc. cit.) are built essentially in the same way, and have strong main axes, carrying alternating bracts in two opposite rows and axillary strobili. There is an earlier, more primitive type, characterized by elongate megasporophylls projecting from the apical region of the strobilus, and a later, reduced type, characterized by very short, unbranched megasporophylls. The strobili are built up of an axis and spirally arranged, homologous scales. Most of these are sterile, and either simple or forked into two lobes, while the remainder are megasporophylls. In the older type, cruciately dichotomized sporophylls arise from the axis, each carrying two terminal but pendulous ovules. The younger type has four to one megasporophylls, each terminated by a single, erect ovule. In addition, the latter type has nonfunctioning sporophylls, each with an aborting megasporangium. The vascular bundle of the megasporophyll branches into three, of which the sporangium receives one and the two apical fusing lobes of the sporophyll forming the integument one each.

Finally, Florin (1936a) investigated the epidermal structure of parallel-veined, cordaiteanlike leaves of mesozoic age, and found that they represented ginkgophytes, conifers, bennettites, or forms of uncertain position, but in no case the cordaites. He concluded that the cordaites are in all probability an exclusively paleozoic group of gymnosperms. It seems probable that they were derived, independently of the pteridosperms, from primitive vascular plants of the general psilophyte type.

Ginkgoales

Gunckel and Wetmore (1946) investigated the origin and development of the cortex, pith, and procambium in *Ginkgo,* the subsequent development of primary xylem and phloem, and the relation of the primary vascular strands to the organization of the shoots. They demonstrated a close relation between the vascular organization and the appearance of foliar primordia on the vegetative apex. Two acropetally developing procambial strands are already projected into the region of a presumptive leaf primordium before this primordium appears. Contrary to previous concepts, the two traces of a leaf have independent origins. The female organ of *Ginkgo* still attracted much attention (Mehra, 1939; Karstens, 1945; Florin, 1949; Nozeran, 1949b; and others). It had variously been considered an axillary inflorescence; an axillary flower; a modified megasporophyll; a dichotomized placenta; the fertile lobe of a trophosporophyll; and an axillary sporangial truss bearing terminal ovules. The collar at the base of the ovule had been interpreted as two fused prophylls of a flower, as the vestige of a true aril, as a megasporophyll, and as an outgrowth on the sporophyll, and the integument as the two fused segments of a perianth, as two fused megasporophylls, as a single megasporophyll, or as the lamina or part of the lamina of a megasporophyll. Florin, who compared *Ginkgo* with *Trichopitys* (cf. below), concluded: The ovulate complex is not an inflorescence (compound strobilus); there are no leaflike megasporophylls or bracts. It might be called a primitive "flower" (simple strobilus or fertile short shoot). The ovulate appendages of its axis have the character of sporangiophores. The "flower" is thus a wholly fertile, dichotomized sporangial truss (syntelome) bearing terminal ovules without any relation to leaves. It corresponds to the female flowers of the cordaites and early conifers, but is not placed in an inflorescence. In Nozeran's opinion, however, the normal biovulate organ is a leaf, inserted on a rudimentary secondary axis, while Gaussen (1944–1952) regarded it as composed of a much-reduced axis carrying one single or two-to-several fused uniovular petioles (carpellary leaves).

Florin (1936a) revised the fossil ginkgophytes and proposed a tentative classification based on the morphology and epidermal structure of the foliage leaves (see also Harris, 1932–1937). Certain genera were studied in respect to the leaf-traces in their short shoots and the internal structure of their leaves. Two groups were discerned, a smaller with petiolate leaves of the *Ginkgo* type, and a larger with wedge-shaped leaves. The latter also differed in the division of the leaves, in the short shoots being deciduous, in having single leaf-traces, etc. The origin of the double leaf-trace in living *Ginkgo,* as described by Gunckel and Wetmore, tends to emphasize the differences between the two groups. The female flowers of a permian ginkgophyte, *Trichopitys,* were found to resemble those of *Ginkgo* in position and general type (Florin, l.c.). Kräusel (1943a, 1943b) re-investigated some mesozoic forms, among which was a species of *Sphenobaiera* with male flowers on short shoots. Their axis is branched into stalklike, bifurcated appendages, carrying erect sporangia terminally. Harris (1942–1952, 1951b) became increasingly doubtful of the correctness of classifying the genera *Czekanowskia* and *Solenites* in the Ginkgoales. On circumstantial evidence he referred to these a type of female fructification, *Leptostrobus,* different from that of any known plant. The larger of the above-mentioned groups of ginkgophytes might thus turn out to be a heterogeneous assemblage.

The Ginkgoales and Cordaitales are probably of a common origin very far back in the history of the vascular plants.

Coniferae

New efforts were made to solve the significant problem of the morphology of the female conifer cones. At first opinions differed as much as ever. Kötter (1931) and Schmid (1937) held to the excrescence theory of Sachs-Eichler. Stefanoff (1936) considered the ovuliferous scale a "cladosperm," homologous to a dichotomized projection of a pteridosperm frond as well as to a leaf of *Cycas* or *Ginkgo.* Pulle (1938) regarded the araucarian cone as uniaxial, and as a primitive form of female strobilus in the conifers. Thomson (1940) agreed to this, and considered the bract and ovuliferous scale components of a megasporophyll. In Chadefaud's (1940) opinion the conifer "carpel" is derived from a prototype analogous to the pinnate megasporophyll of *Cycas,* and composed of a rachis and uniovulate pinnae. The ovuliferous scale developed by fusion of the pinnae, while the main part of the sporophyll formed the bract. Kujala (1942) and Hiitonen (1950) embraced the foliolar theory of Delpino and Penzig. Arber (1950) regarded the ovuliferous scale as made up of two fused leafy outgrowths from the axillant bract. Hirmer (1936) and Propach-Gieseler (1936) investigated the ontogeny and comparative morphology of the female cones of living conifers, and arrived at the conclusion that the ovuliferous scale and the bract result from a serial splitting of one single member. The fertile part of the megasporophyll was believed to derive from a peltate perisporangiate structure. Other morphologists professed, in one form or another, the brachyblast concept of the ovuliferous scale. To begin with, this applies to Sahni and Singh (1931) and Doyle and O'Leary (1934), who investigated the female cones of *Fitzroya.* The latter authors noted that the cone structure is a very ancient feature, the origin of which must be sought in the reduction of the primitive nonlaminated reproductive branching systems of early vascular plants. Goebel (1932) maintained his earlier conception, and Lanfer (1933) supported his view. On the basis of ontogenetic studies of female conifer cones Hagerup (1933, 1934) arrived at the conclusion that those of the Taxodiaceae, Pinaceae, Podocarpaceae, Araucariaceae, and Cupressaceae are in the nature of inflorescences. Exceptions are the Taxaceae and certain Juniperoideae. A cone and a long shoot of the pine are similarly constructed. In the cone a short secondary axis develops axillary to each bract. It carries two prophylls, and above them a median leaf on the posterior side, which is the "ovuliferous scale." The construction is similar in other families, but the number of leaves on the floral axis varies. The integument is considered a megasporophyll; it develops a basal megasporangium (nucellus) on its morphological upper side. In the uniovulate flowers of *Araucaria* and *Dacrydium,* Hagerup postulated the presence of sterile prophylls, while in *Cupressus* there would be no sterile leaves at all, and consequently no ovuliferous scale. *Juniperus* has lateral as well as terminal flowers, inflorescences as well as single flowers; the sporophyll (integument) may be terminal on the main axis. In the taxads, too, the integument was believed to be a sporophyll. Already Lanfer (1934) however, criticized his interpretation of the integument, and so did later other morphologists, while Emberger (1944) accepted it. Satake (1934), Doak (1935), Wettstein (1935), and Chamberlain (1935) were adherents of the brachyblast interpretation.

The persistent diversity of opinions convinced Florin (1938–1945, 1951) that this problem could hardly be definitely solved by investigations on living conifers alone, and that the fossil material so far considered had not been sufficiently old to reveal the primary organization of their female organs. He therefore took up a comparative morphological study of the cones of fossil and living conifers. It was found that the paleozoic cordaites and conifers furnished the main clue to the interpretation of the cones of mesozoic and more recent conifers. Primarily, the fertile complex is a radially symmetrical short shoot in the axil of a bract, and has the character of a strobilus or flower. In the most ancient conifers (Lebachiaceae) the floral axis carries several sterile scales and one to a few megasporophylls, each with one terminal orthotropous, erect ovule. The younger types of cones have arisen by transformation of this primitive organization. The axis of the flower became reduced. Its symmetry was changed very early, the megasporophylls becoming confined to the posterior side of the axis, and the whole short shoot flattened. Disregarding for the moment the *Ernestiodendron* type, the paleozoic and mesozoic conifer cones are characterized by a gradual modification and differentiation of the axillary complex into a fertile part facing the cone axis, and a sterile part—the "ovuliferous scale." The sterile scales and the sporophylls on the axis concurrently changed from a spiral to a decussate arrangement. Not only the sporophylls, but also the sterile scales, were moreover confined to the posterior side, including the flanks, of the flower axis, while the anterior sector became wholly suppressed. The number of sterile scales was reduced until finally only one was sometimes left. In the paleozoic *Ernestiodendron* type, too, the primary seed-scale complex was radially symmetrical, containing numerous sterile scales and a few sporophylls, but in connection with the flattening the sporophylls were favored at the expense of the sterile scales. The reduction of the flower thus took a somewhat different course in this case, and had already in the lower permian led to the development of wholly fertile seed-scale complexes. The evolution of the female conifer flower presents some further features of interest. In some cases the number of sporophylls was reduced to one, as seen in *Lebachia*, but usually there were at least two sporophylls to each flower. The sporophylls themselves became more and more reduced, and finally became completely incorporated in the "ovuliferous scale." Various other parts became fused, e.g., the sterile scales along their margins, the sporophylls at their bases, and the "ovuliferous scale" to the bract. The ovules were always orthotropous, seated singly and terminally on lateral megasporophylls. They were first erect but from the upper permian onwards mostly inverted. The female cones of living conifers are directly connected with those of the mesozoic and paleozoic types. Disregarding such changes as a shortening of the internodes of the cone axis and a reduction in the number of its appendages, the great morphological diversity in the female sex is due to the modification in various directions of the axillary fertile short shoot and its accompanying bract. The comparative study of living conifers disclosed additional trends involved in the evolution of the female conifer cone, relating to external as well as anatomical features. The genera *Palaeotaxus*, of early mesozoic age, *Taxus*, ranging from mesozoic to recent times, and other still living taxads differ, however, from all true conifers by having solitary flowers. Their ovules are seated terminally, on the flower axis itself, and megasporophylls are accordingly absent. The flowers of these genera can therefore not be derived from those of the paleozoic cordaites or conifers.

Hirmer (1941), Wilde (1944), P. Bertrand (1947), Lam (1948, 1952), Gaussen (1948, 1944–1952), Wilde and Eames (1948, 1952), as well as Mägdefrau (1942)—a former supporter of the excrescence theory—were convinced of the correctness of the brachyblast conception of the female conifer cones (cf. Eames, 1913). Lam considered these stachyosporous by nature, while in the majority of genera the male organs are phyllosporous. He also admitted that *Taxus* stands apart from the true conifers, but did not consider the differences fundamental. According to Wilde and Eames (1948), evidence of vascular anatomy supports the view that the single ovule on the cone scale of *Araucaria Bidwillii* is a survivor of three, and that this cone may be derived from the mesozoic *Schizolepis* type. Janchen (1949) appears to prefer Wettstein's and Herzfeld's view of the nature of the ovuliferous scale. Besides Florin (l.c.), Harris (1932, 1937, 1943), Hörhammer (1933), Hirmer and Hörhammer (1934), Kräusel (1938, 1952), Kon'no (1944), Wieland (1935), and others, have studied the morphology of various female conifer cones of mesozoic age. *Elatides Williamsoni* was shown by Harris to be a member of the Taxodiaceae, the oldest yet known, and typical araucarian cones were also found.

Studies of the conifer male organs have been carried out by Goebel (1932), Doyle and O'Leary (1934), Dluhosch (1937), Thomson (1940), Florin (1938–1945, 1951), and Wilde (1944). The paleozoic genera differ from the cordaites by the flower axis bearing in its fertile region exclusively microsporophylls, which are hypopeltate, hyposporangiate, and bisporangiate. Pilger (1926, 1929), Goebel, and Wettstein (1935) regarded the laminate, hyposporangiate sporophyll as the basic form, and its subpeltate form in some Cupressaceae as an advanced condition, while to Dluhosch the basic form was a peltate, centrally petiolate, and perisporangiate sporophyll, and the dorsiventral, hyposporangiate form advanced. According to a third view (Doyle and O'Leary, Zimmermann, 1930, Florin), the microsporophylls originated from a radial sporangial truss with terminal, erect sporangia, the laminate sporophyll represents a derived condition, and the peltate perisporangiate sporophyll is an intermediate stage, but has probably never occurred in the true conifers. Sporophylls with several free sporangia and a well-developed vascular bundle system are held to be more primitive than those with few sporangia fused to the basal portion of the sporophyll and a weak bundle system. Wilde believed that the simple male cone as found today in most conifers is a single surviving terminal unit of a fertile branch that was once compound like the female. The organization in *Cephalotaxus* appeared to Nozeran (1949a) to unite in a single individual different stages of evolutionary development, viz., a successive reduction of the secondary axis and a transfer of the reproductive function from the appendages of this axis to those of the primary axis, which correspond to the normally axillant bracts. Finally, Allen (1946a) found the generally accepted concept of a hypodermal origin of the microsporangium open to doubt.

Boureau (1949; cf. Gaussen, 1952) studied the alternate tracheary pitting in coniferous secondary wood, and distinguished three main types, viz.: (1) the primitive multiseriate type of paleozoic age (*Dadoxylon*); (2) the uniseriate type, appearing in early mesozoic time, or still earlier, and sometimes resembling the type of pitting of the Pinaceae; and (3) a late, overevolved multiseriate type, still present in the living Araucariaceae. He is of the opinion that a pinaceous evolutionary branch originated at the end of the paleozoic era. Several mesozoic woods are intermediate between *Dadoxylon* and modern Pinaceae. The Gothan school interpreted them as forerunners of the Pinaceae, showing traces of araucarian or cordaitean ancestry (Protopinaceae), while the Jeffrey school considered them primitive araucarians of pinaceous ancestry (Araucariopityaceae). Bailey (1933) found similar combinations of characters in living conifers, e.g., *Cedrus* and *Keteleeria,* and concluded that certain Protopinaceae fall within the range of structural variability of living Abietoideae and others within the range of variability of the Podocarpaceae, Taxodiaceae, and Cupressaceae. Bailey and Faull (1934) stressed the point that the lack of information on the limits of structural variability is the cause of the unsatisfactory classification of fossil coniferous woods. Most anatomical features utilized for diagnostic purposes—even such as the pitting of rays and of wood parenchyma, and the contiguity and alternation of tracheary pitting—vary in different trees, and not least in different parts of a single tree. Similar studies were later carried out, particularly by Bannan (1941a, 1941b, 1942, 1944, 1952), on various Pinaceae and Cupressaceae. Kräusel (1949b) was aware that the investigation of the wood structure in recent conifers could not be regarded as completed and that the value of certain structural features used for identifying and classifying woods was not absolute. But there were no sufficient reasons for an attitude as sceptical as that of Bailey. Kräusel insisted on the unique position of the Protopinaceae as combining araucarian features with characters of other conifers and often showing a transitional tracheary pitting. He admitted, however, the impossibility of solving the old problem of the relative geological age of the Araucariaceae and the Pinaceae on the basis of wood structure alone. All that could be said was that the araucarian type of wood is older than the pinaceous type. Bannan (1933, 1936) studied the formation and distribution, in the Pinaceae, of vertical resin ducts in the secondary wood, which were found always to be the effects of environmental influences. In the individual species the development of resin tissue increases from the seedling to the adult tree, and outwards from the pith in both. Jeffrey's theory of the pinelike distribution of ducts as the primitive type is not supported by the fossils. A phylogenetic enlargement of the response to injury is instead indicated. The identification and classification of coniferous woods in general was also dealt with by Slyper (1933), Yarmolenko (1933), Record (1934), Peirce (1936, 1937), Phillips (1941), and Greguss (1950, 1951), and numerous special studies were carried out. Sterling (1947) summarized our knowledge of the distribution of sclereids, and Buchholz and Grey (1948, 1951) investigated their distribution in the leaves of *Podocarpus* species.

The occurrence and condition of axillary buds were investigated by Holthusen (1940), who found that macroscopically bare leaf axils do not contain any embryonic cells or meristematic tissue. Conifers with long and short shoots have as a rule a bud primordium in each leaf axil on the former. The apex of a short shoot of the pine is a slender, only slightly vaulted cone; the needles have no axillary meristem. Doak (1935) considered *Cedrus* more primitive than *Pinus,* but Flous (1936b, 1938a) denied the supposed homology of the short shoots. Gaussen (1944–1952) distinguished in general between auxiblasts (rapidly growing long shoots), mesoblasts (long shoots of more tardy growth), and brachyblasts (short shoots), and characterized the "short shoot" of *Cedrus* as a mesoblast.

In respect to the conifer foliage leaves, Gaussen (l.c.) distinguished euphylls and pseudophylls, the latter identical with the adult pine needles. The polymorphy of the leaves in this genus was especially investigated by him and his students, and by Doak (1935). An interesting feature in *Metasequoia* (Stebbins, 1948; Morley, 1948; Sterling, 1949) is the decussate phyllotaxy, with the leaves of the deciduous short shoots spreading out in one plane by the rotation in opposite directions of alternating nodes of the axis and a simultaneous bending of the leaf bases. Goebel (1932) arranged the types of conifer leaves in a series: (1) forking of bundles in the cortex as well as in the lamina (*Agathis*); (2) forking in the cortex only (certain araucarias); (3) only a single forking, occurring in the cortex (*Pinus*); (4) no forking at all. Large leaves were placed at the beginning, and small, narrow leaves at the end. Florin (1938–1945, 1951), however, distinguished two different types of transformation by reduction of primitive many-veined conifer leaves into uninerved leaves, one based on the conditions in the living Araucariaceae, and the other on those in paleozoic conifers. The latter type, which illustrates the probable evolution of the leaf in the majority of conifer families, is characterized by the direct reduction of a but little complicated, cruciately dichotomized telome system (syntelome) and the foliarization of the single remaining mesome. The anatomy of the leaves of living conifers was described in many cases, mostly for the purposes of specific identification and classification.

As regards the history of the Coniferae, Florin (1938–1945, 1951) investigated the upper carboniferous and lower permian conifers, with special reference to the genera *Lebachia* and *Ernestiodendron,* which he classified in a new family, the Lebachiaceae. Both the vegetative and reproductive organs of these genera were treated, and other less completely known types were also described, including the upper paleozoic genus *Walkomiella* (Florin, 1940a). Conifers of triassic and jurassic age were discovered, or became better known, by the efforts of several investigators, who made use of the epidermal structures whenever possible. Of particular value is the extension in recent years by Harris (1942–1952, 1943) and his students of our knowledge of the conifers in the British jurassic flora. Penny (1947) continued the work of Hollick and Jeffrey (1909) on lignitic material of upper cretaceous conifers. He admitted that *Brachyphyllum* and *Brachyoxylon* may be related to the Araucariaceae, although the contiguous type of tracheary pitting occurs with no greater frequency than in several modern genera of the Taxodiaceae and Cupressaceae. Contrary to earlier opinions, the internal structure of certain pine leaves was held to correspond essentially to that of modern *Haploxylon* pines. Hollick and Jeffrey had concluded that *Geinitzia* was of araucarian affinity, but Penny found no araucarian features except the lack of resin parenchyma. The type of wood, the presence of resin parenchyma, and the character of the ray cell, moreover argued against the opinion that *Widdringtonites* could be araucarian. *Frenelopsis* was shown to have the *Cupressinoxylon* type of wood, which confirmed the position of the genus suggested by studies of the leaf epidermis (Carpentier, 1937; Romariz, 1946). It is closely related to, if not identical with, the genus *Tetraclinis,* to which also certain isolated woods are believed to belong (Grambast, 1951). Florin (1940b) found in the coniferous floras of southern lands, including peninsular India, a total absence of now-living typically northern genera of Cupressaceae (cf. H.-L. Li, 1953), of Taxodiaceae (except *Athrotaxis*), of Pinaceae and Cephalotaxaceae, of Taxaceae (except one *Torreya*-like form and presumably also of *Austrotaxus*), and of several extinct genera discovered in northern lands. From the permian onwards, the southern conifer floras appear to be distinguished by pronounced features from contemporaneous northern floras. The results contradicted the opinions of Studt (1926) that all conifers originated in the northern temperate zone or in the arctic regions. Numerous special studies of tertiary fossil conifers have been carried out, but a few examples of recent developments will have to suffice here. Szafer (1949) investigated the genus *Tsuga* in Europe, and indicated its probable evolution. Miki (1941) discovered a new genus of the Taxodiaceae, *Metasequoia,* which was subsequently found not only to have been widely distributed in the northern hemisphere in late cretaceous and tertiary times (Chaney, 1951), but also to be represented by a living species native of China (Hu and Cheng, 1948; cf. Florin, 1952a). Recent contributions to our knowledge of the history of the genus *Sciadopitys* have proved that this played an important role in the tertiary vegetation of central Europe (Mädler, 1939; Thiergart, 1949; Kirchheimer, 1950). A considerable number of papers were also published on fossil woods, which (with the exception of *Araucarioxylon*) were critically enumerated by Kräusel (1949b) as a complement to his earlier publication on the same subject.

There has been much discussion of the taxonomic arrangement of certain living generic groups of conifers. This applies to the Pinaceae (Flous, 1936a, b; 1938a, 1938b; Ferré, 1939, 1942, 1943; Ferré and Gaussen, 1945; Campo-Duplan, 1950; and Gaussen, 1944–1952). The Toulouse school regards *Pinus* as the most primitive genus in the family. The remaining genera are arranged as follows: (1) *Cedrus-Abies,* (2) *Pseudolarix-Keteleeria,* (3) *Larix-Pseudolarix,* (4) *Picea,* and (5) *Tsuga.* Other classifications have been proposed by Yarmolenko (1933), Janchen (1949), and Sugihara (1947). *Sciadopitys* is often regarded as the representative of a family of its own (see Janchen, 1949; Takhtadjan, 1950; Johansen, 1951). A few authors have proposed the segregation of the family Taxodiaceae into several independent families (see Janchen, 1949; Sugihara, 1947), while the majority have retained it in its earlier sense—except for the exclusion in some instances of *Sciadopitys* as mentioned above—and instead divided it into several subgroups. There are similar differences of opinion on the classification of the Cupressaceae, and here, too, new families have been proposed (see Janchen, 1949; Sugihara, 1947), while in other cases subfamilies are discerned (H.-L. Li, 1953, etc.). The Podocarpaceae in the usual sense may also comprise genera of widely varying affinities (Buchholz, 1934; Johansen, 1951). These discrepancies are in the main due to our still incomplete and unsatisfactory knowledge of the true affinities of the various conifer genera.

The class (or order) Coniferae at large has either been classified directly in a series of groups of family rank, or attempts have been made to discern orders (or suborders). Janchen (1949) and Neger, Münch and Huber (1952) distinguished the orders Taxales (Taxoideae) and Pinales (Pinoideae), thus adhering in principle to the old artificial subdivision of the conifers into the two families Taxaceae and Pinaceae. Gaussen's (1944–1952) system has three suborders: (1) Taxineae, with the Taxaceae; (2) Podocarpineae, with the Podocarpaceae; and (3) Pinoidineae, with the remaining families. The Podocarpineae and Pinoidineae were considered two different evolutionary branches derived from the "paleoconifers." Pulle (1937, 1950), however, has introduced quite a different system for the conifers, including no less than five orders, viz., the Araucariales, Podocarpales, Pinales, Cupressales (with Taxodiaceae and Cupressaceae), and Taxales (with Cephalotaxaceae and Taxaceae). In this system Florin (*in* H. Erdtman, 1952) has proposed that the Taxaceae be removed from the conifers and raised to the rank of an independent class, and that the Cephalotaxaceae be raised to the rank of a separate order of the Coniferae.

Taxales

Sahni (1920) expressed the opinion that the taxads were so distinct from the true conifers that they deserved to rank as a separate phylum, Taxales. Besides some studies of gametophytes and embryogeny, contributions toward our knowledge of the taxads have in recent years been made, *inter alia,* by Saxton (1934) in respect of the reproductive organs of *Austrotaxus,* by Wilde (1944) of the male organs of *Austrotaxus* and *Amentotaxus,* and by Phillips (1941) and Greguss (1951) of the structure of the secondary wood of these genera. According to Florin (1938–1945, 1948a 1948b, 1951), the living taxads represent five genera, viz., *Taxus, Torreya, Nothotaxus, Amentotaxus,* and *Austrotaxus.* Reproductive organs of fossil taxads have so far only been studied in *Paleotaxus* of triassic age and in a *Taxus* of jurassic age. Florin found that in certain respects the taxads are clearly apart from the true conifers. In the taxads the ovule is always a direct continuation of the "flower" axis, while in the conifers it is terminal on lateral appendages (megasporophylls) of the corresponding axis. In contradistinction to the conifers (and cordaites), they have single female "flowers" placed axillary on sometimes greatly reduced vegetative shoots, and always also bear erect ovules, each enclosed by an aril. The male flowers are remarkable for the radially symmetrical, perisporangiate sporophylls of certain genera, and for the gradual change from this form to a dorsiventral structure in others. On these grounds Florin agreed to the exclusion of the taxads from the Coniferae (cf. McLean and Ivimey-Cook, 1951, and Rothmaler, 1951–1952).

Chlamydospermae

According to Hagerup (1934) there are mainly four earlier interpretations of the appendages of the axis of a female flower in this group: (1) at least one of the envelopes is in the nature of an aril; (2) the envelopes are integuments; (3) the envolopes are the leaves of a perianth; (4) one or more envelopes are sporophylls. In his opinion all envelopes are by nature leaves. The female flowers are placed axillary to a bract on a mother axis, and made up of a short lateral axis carrying a terminal ovule surrounded by one or two envelopes. The lowest of these is formed by two prophylls. The megasporophyll (integument) is seated on the tip of the floral axis, surrounded by false carpels forming a cuplike envelope. The axis of a male *Ephedra* flower carries four leaves, of which two prophylls and a fourth leaf form between them the perianth, and a third leaf, situated at the apex of the axis, is the stamen. According to Lam (1948), however, all chlamydosperms are stachysporous in both sexes. Eames (1952) considered Hagerup's interpretation of *Ephedra* partly inaccurate. The ovulate and microsporangiate cones were found to be strictly homologous. The cones consist of decussate pairs of bracts borne on short axes. Axillary to some of these bracts there are fertile axes, each with a pair of free or connate bracteoles. The microsporangiate shoot carries two transversal sporophylls above the bracteoles. In primitive species the microsporophylls are free, and the axis may project beyond their bases, while in most species they are connate above the axis tip, and form a column. The synangium is probably a two-chambered sporangium. The reduced ovulate shoot has connate bracteoles loosely appressed to the ovule, forming an envelope. The ovule is placed terminally on a much-reduced megasporophyll. The sporangia have been reduced, phylogenetically, to one on each sporophyll in both sexes. In his view, *Ephedra* is an isolated surviving derivative of the ancestral cordaites and conifer stock. The terminal positions of the *Welwitschia* and *Gnetum* ovules on the shoot axes were considered by Eames a conclusive indication of a phyletic gap between these genera on the one hand, and *Ephedra* on the other.

Fagerlind (1946) regarded the fertile shoot system of *Gnetum* as composed of an axis and whorls of bracts. Axillary to these bracts there are collarlike, continuous swellings, on which the male and female flowers (reduced short shoots) are produced. Three integumentlike appendages appear on the floral axis, the apex of which is occupied by the nucellus. Similarly, the male flower has a perianth and a central, often dichotomized, stamen. The strobilus and the male and female flowers are homologous, in the main differing only in the degree of development of the axes and axial appendages. The bracts relate to their productive swellings in the same way as do the bract whorls to the parts of the strobilus situated above them. In this connection Fagerlind amplified the telome theory in the following way. The stem is a columnar syntelome composed of radial, parallel telomes or telome sympodia. Appendages arranged in whorls or spirals are formed by simultaneous and successive bifurcations respectively. The inner of the resulting telomes build up a new columnar syntelome, while the remainder form an outer collarlike syntelome, which may later split into several parts. The leaf pairs, the bract whorls, and the envelopes of the male and female flowers in *Gnetum* are more or less deeply split collarlike synetelomes, while the shoot apex, the productive swelling, the nucellus, and the primordium of the stamen are columnar syntelomes.

Eames's views of the probable origin and interrelationships of the chlamydosperms differ radically from those of Lavier-George (1935). In her opinion the line of division runs between on the one hand *Welwitschia* and *Ephedra,* which both show affinity to the gymnosperms in foliar and caulinar features, and on the other, *Gnetum,* which resembles the dicotyledons in the same respects. The presence in all three genera of a medullosean stem structure in course of regression, and of centripetal xylem, indicates that the chlamydosperms derive wholly from the base of the pteridosperm stock. These and other divergences of opinion are reflected in the taxonomic treatment of the chlamydosperms. An older type of arrangement is that of Gaussen (1944–1952), who regards them as forming a single class and order composed of three families. Other investigators have two orders (Pulle, 1937, 1950; Arnold, 1948), while a third group (Skottsberg, 1940; Takhtadjan, 1950; Lawrence, 1951; and Eames, 1952) considers each of the families to deserve ordinal rank: Ephedrales, Welwitschiales, and Gnetales. Rothmaler (1951, 1951–1952) even went so far as to raise these to the rank of classes, of which that of the Ephedropsida was referred to the stachyosperms and the remaining two to the chlamydosperms.

Classification of the Gymnosperms

Danser (1950) emphasized that the modern conception of systematics as the theory of the classification of life cycles, rather than of objects, necessitates consideration of various matters otherwise often regarded as belonging to other sciences, as long as these are useful for classification purposes. The present review is worked out from this point of view. Owing mainly to the progress in paleobotany and comparative morphology in the widest sense, the last decades have seen great progress in our knowledge of the actual chronological succession, the evolutionary history, and the interrelationships of the several gymnosperm groups. This has not failed to affect their phylogenetic or vertical classification. The pteridosperms and the cordaites are both groups of very great antiquity. The cycads, ginkgoes, conifers, and probably the taxads, are also fairly old, while the bennettites, Pentoxylaceae, Peltaspermaceae, Corystopermaceae, and Caytoniaceae are still unknown from paleozoic times. The chlamydosperms have not yet been recognized with certainty except in tertiary strata. Looked upon as a whole, the gymnosperm division of the cormophytes evolved progressively during the carboniferous, Permian, Triassic, and Jurassic periods, while from the Cretaceous onwards it has been characterized by relative stability.

Of late years it has been realized to an ever-increasing extent that the classification of the vascular plants in cryptogams and phanerogams, and in pteridophytes, gymnosperms, and angiosperms is not natural. It is horizontal in character, and records different levels or phases of general organization instead of expressing natural relationships. We have thus arrived at a point where the term Gymnospermae of the nineteenth century is often regarded as obsolete, and therefore abandoned. According to an extreme view, each of the main groups of gymnosperms represents a separate evolutionary line (P. Bertrand, 1947; Bertrand and Corsin, 1938). According to Halle (1937) the evolution of the seed-plants has probably, since an early date, proceeded along at least two divergent main lines, viz., one in which the seeds and sporangia became localized to leaves of the megaphyllous type, and another in which the plant body was differentiated into a vegetative and a reproductive region, the spore-producing members congregating to form "inflorescences" or "flowers," and the terminal position of the ovules and sporangia retained for a long time. The cordaites, appearing early in the history of the higher plants, represent an offshoot of this second series. In Arnold's (1948) opinion the gymnosperms (*minus* the chlamydosperms) are composed of two separate groups of high rank, the cycadophytes and the coniferophytes, distinguished by features that have characterized them as far back as they can be traced. Contrary to Halle, Arnold referred both cycads and cycadeoids to the cycadophytic line. As mentioned earlier, Sahni (1920, 1948) divided the gymnosperms into phyllosperms and stachyosperms, but Schoute (1925) and Eames (1952) did not think this measure justified. Lam (1948, 1952), however, extended Sahni's idea of the discrimination between phyllosperms and stachyosperms within the Gymnospermae to comprise all vascular plants of both sexes, and regarded stachyospory and phyllospory as important factors in the system of the cormophytes. Phyllospory, or the position of the sporangia on many-telomed sterile fronds, i.e., true sporophylls, is regarded as the advanced condition, and stachyospory—where the sporangia, originally axis-borne, are not, or hardly at all, connected with sterile telomes or syntelomes except by secondary processes—as the primitive feature. There are strictly stachyosporous and fully phyllosporous groups of plants, but also groups of a mixed nature. Lam's views, too, have been negatively criticized by Takhtadjan (1950) and Eames (1951), but he maintains them even in his latest publications.

Turning now to particulars of the more recently propounded systems (Schaffner, 1934; Wettstein, 1935; Engler and Diels, 1936; Pulle, 1937, 1950; Skottsberg, 1940; Tippo, 1942; Gaussen, 1944–1952; Arnold, 1948; Lam, 1948; Emberger, 1949, 1952b; Chadefaud, 1949; Johansen, 1950, 1951; Němejc, 1950; Takhtadjan, 1950; Florin *in* H. Erdtman, 1952; McLean and Ivimey-Cook, 1951; Rothmaler, 1951, 1951–1952; Neger, Münch and Huber, 1952; cf. Florin, 1952b), it is, as already indicated, a striking feature of some of them that the traditional taxon Gymnospermae has been either discarded, or its circumscription altered. The presence of naked seeds (or ovules) is an attribute which has begun to lose prominence. In Lam's system, which divides the Cormophyta into four main groups on the grounds of morphology and phylogeny, the Gymnospermae (except the pteridosperms and chlamydosperms) are called Mesocormophyta. Emphasizing a presumed polyphyletism of the Gymnospermae (in the old sense), Arnold proposes to substitute for this division three independent groups of equivalent order, viz., the Cycadophyta, Coniferophyta, and the Chlamydospermophyta, while Rothmaler has Gymnospermophytina (pteridosperms and cycads), Stachyospermophytina (including the ephedras), and Chlamydospermophytina (including the bennettites). Johansen agrees in principle with Arnold, but replaces the Gymnospermae by an even greater number of phyla or divisions—the Pteridospermophyta, Cycadophyta, Ginkgophyta, Coniferophyta, and the Ephedrophyta (chlamydosperms). The phylum Ginkgophyta contains the orders Cordaitales and Ginkgoales, which in Arnold's system were included in the Coniferophyta. Emberger deals with the gymnosperms in another way. He stresses the different kinds of "seeds," in the first place differentiating between Praephanerogamae and Phanerogamae. The former are regarded as a major group, intermediate between the vascular cryptogams and the phanerogams. His classification appears to be intentionally horizontal, and consequently nonphylogenetic. The pteridosperms in the wide sense, and the cycads, cordaites, and ginkgoes, are said to be praephanerogams, while the conifers, taxads, bennettites and chlamydosperms—being true gymnosperms—are referred to the phanerogams. In this way the cordaites and ginkgoes have been far removed from the conifers, with which they are otherwise usually considered to be rather closely related. And whatever the natural position of the megaphyllous bennettites might be, this group has little to do with the microphyllous conifers. Whenever a subdivision named Cycadophyta (Cycadopsida, Cycadomorphae, Phyllosperminae) of the gymnosperms (or of the Pteropsida in the wide sense, the phanerogams, and the mesocormophytes, respectively) has been proposed in recent years, both the Cycadinae (Cycadales) and the Bennettitinae (Bennettitales, Cycadeoidales) have, with one exception (Rothmaler), been referred to this. Whether the relationship between these two groups is really as close as thus often assumed is a question, which can hardly be settled without a satisfactory knowledge of the nature and early evolution of the bennettitinean gynoecium. Disregarding the chlamydosperms (gnetophytes or ephedrophytes), Gaussen's system has two subdivisions of the Gymnospermae, viz., the above-mentioned Cycadophyta and Coniferophyta. The latter corresponds in the main to the Stachyospermae of Sahni. Besides the cycads and the bennettites, the Cycadophyta *sensu* Gaussen include the pteridosperms in the wide sense, and Sahni's Pentoxylaceae. A similar arrangement is adopted in the systems of Lam, Arnold, Chadefaud, Němeje and Rothmaler, although Chadefaud's Cycadomorphae and Němejc's Cycadophyta also include the chlamydosperms, and Rothmaler refers the bennettites to the latter group. Takhtadjan has divided the gymnosperms into four subclasses, viz., the Pteridosperminae, the Phyllosperminae, the Stachyosperminae, and the Chlamydosperminae. Finally, in the system of Pulle the gymnosperm classes (or orders) have not been brought together into subdivisions of higher rank, and the pteridosperms are kept separate from them.

The consensus on the phylogenetic classification of the gymnosperms is thus by no means complete. Reasons for this are not difficult to find. The paleobotanical evidence, after all, is still in many cases inadequate to justify a decision between one view and the other. Additional information is required, particularly on the paleozoic and mesozoic pteridosperms, the early bennettites and the Pentoxylaceae, and on many other plants of mesozoic age. It is moreover often difficult to distinguish primitive from advanced characters, and to trace the origin and evolution of the latter. There has been, to a considerable extent, parallel and convergent evolution in the Cycadophyta and the Coniferophyta, and similar types of structure have originated in diverse groups at the same or different times. The evaluation of characters or groups of characters for taxonomic purposes sometimes varies considerably. Further progress in this field appears to require not only continued and intensified accumulation of new data, but also a new, unprejudiced analysis and synthesis of the implications of all available facts. The possibility of increasing the efficacy of the methods of approach applied to the study of the phylogeny of the gymnosperms is by no means exhausted. In the last hundred years they have gradually allowed us to acquire an immensely valuable insight into the main historical steps and events of the evolutionary process. The edifice of phylogenetic classification, is, as Sprague (*in* Huxley, 1940) wrote, subject to continual pulling down and rebuilding, but many foundation stones remain in position, and the permanent structure is steadily growing.

BIBLIOGRAPHY I.

Aase, H. C.

1915. Vascular anatomy of the megasporophylls of conifers. Bot. Gaz., 60:277–313.

Abbema, T. van

1934. Das Transfusionsgewebe in den Blättern der Cycadinae, Ginkgoinae und Coniferae. Rec. Trav. Bot. Néerl., 31:309–390.

Allen, G. S.

1946a. The origin of the microsporangium of *Pseudotsuga*. Bull. Torrey Club, 73:547-556.

1946b. Embryogeny and development of the apical meristems of *Pseudotsuga*. I. Fertilization and early embryogeny. Amer. Journ. Bot., 33:666–677.

Anderson, E.

1937. Cytology in its relation to taxonomy. Bot. Rev., 3:335–350.

Andersson, E.

1947. A case of asyndesis in *Picea Abies*. Hereditas, 33:301–347.

Andrews, H. N.

1940. On the stelar anatomy of the pteridosperms, with particular reference to the secondary wood. Ann. Mo. Bot. Gard., 27:51–118.

1942. Contributions to our knowledge of American Carboniferous floras. I. *Scleropteris*, gen. nov., *Mesoxylon* and *Amyelon*. Ann. Mo. Bot. Gard., 29:1–18.

1945. Contributions to our knowledge of American Carboniferous floras. VII. Some pteridosperm stems from Iowa. Ann. Mo. Bot. Gard., 32:323–360.

1948. Some evolutionary trends in the pteridosperms. Bot. Gaz., 110:13–31.

Arber, A.

1950. The Natural Philosophy of Plant Form. xiv + 247 pp. Cambridge: Cambridge Univ. Press.

Arnold, C. A.

1930. The genus *Callixylon* from the Upper Devonian of central and western New York. Pap. Mich. Acad., 11:1–50.

1938–1948. Palaeozoic seeds. I–II. Bot. Rev., 4:205–234; 14:450–472.

1947. An Introduction to Paleobotany. xi + 433 pp. New York and London: McGraw-Hill.

1948. Classification of gymnosperms from the viewpoint of paleobotany. Bot. Gaz., 110:2–12.

BAILEY, I. W.

1919. Structure, development, and distribution of so-called rims or bars of Sanio. Bot. Gaz., 67:449–468.

1925. Some salient lines of specialization in tracheary pitting. I. Gymnospermae. Ann. Bot., 39:587–598.

1933. The cambium and its derivative tissues. VII. Problems in identifying the wood of Mesozoic Coniferae. Ann. Bot., 47:145–157.

1940. The walls of plant cells. *In* The Cell and Protoplasm. Publ. Amer. Assoc. Advancem. Sci., 14:31–43.

BAILEY, I. W., and A. F. FAULL

1934. The cambium and its derivative tissues. IX. Structural variability in the redwood, *Sequoia sempervirens*, and its significance in the identification of fossil woods. Journ. Arnold Arb., 15:233–254.

BAILLON, H.

1860. Recherches organogéniques sur la fleur femelle des Conifères. Ann. Sci. Nat. Bot., ser. 4, 14:186–199.

1864. Nouvelles recherches sur la fleur femelle des Conifères. Adansonia, 5:1–16.

BAKER, R. T., and H. G. SMITH

1910. A Research on the Pines of Australia. Tech. Ed. Ser., Tech. Mus., New South Wales. No. 16. xiv + 452 pp.

BANCROFT, N.

1914. Pteridosperm anatomy and its relation to that of the cycads. New Phytol., 13:41–68.

BANNAN, M. W.

1933. Factors influencing the distribution of vertical resin canals in the wood of the larch—*Larix laricina* (Du Roi) Koch. Trans. Roy. Soc. Canada, ser. 3, 27(sec. 5):203–218.

1934. Origin and cellular character of xylem rays in gymnosperms. Bot. Gaz., 96:260–281.

1936. Vertical resin ducts in the secondary wood of the Abietineae. New Phytol., 35:11–46.

1941a. Variability in wood structure in roots of native Ontario conifers. Bull. Torrey Club, 68:173–194.

1941b. Wood structure of *Thuja occidentalis*. Bot. Gaz., 103:295–309.

1942. Wood structure of the native Ontario species of *Juniperus*. Amer. Journ. Bot., 29:245–252.

1944. Wood structure of *Libocedrus decurrens*. Amer. Journ. Bot., 31:346–351.

1952. The microscopic wood structure of North American species of *Chamaecyparis*. Canad. Journ. Bot., 30:170–187.

BARTHELMESS, A.

1935. Über den Zusammenhang zwischen Blattstellung und Stelenbau unterer besonderer Berücksichtigung der Koniferen. Bot. Archiv, 37:207–260.

BARY, A. DE

1877. Vergleichende Anatomie der Vegetationsorgane der Phanerogamen und Farne. *In* W. Hofmeister, Handbuch der physiologischen Botanik, 3:1–663. Leipzig: W. Engelmann.

BATTAGLIA, E.

1951. The male and female gametophytes of angiosperms—an interpretation. Phytomorphology, 1:87–116.

Baxter, R. W.

1949. Some pteridosperm stems and fructifications with particular reference to the Medullosae. Ann. Mo. Bot. Gard., 36:287–352.

Belajeff, W. C.

1891–1893. Zur Lehre von dem Pollenschlauche der Gymnospermen. I–II. Ber. Deutsc. Bot. Ges., 9:280–286; 11:196–201.

Benson, M.

1904. *Telangium Scotti,* a new species of Telangium (Calymmatotheca) showing structure. Ann. Bot., 18:161–177.

Bentham, G., and J. A. Hooker

1880. Genera plantarum, 3(1):417–447. London: Lovell Reeve and Co.

Bernard, C.

1904. Le bois centripète dans les feuilles de Conifères. Beih. Bot. Centr., 17:241–310.

Berry, E. W.

1917. The classification of vascular plants. Proc. Nat. Acad. Sci., Washington, 3: 330–333.

1920. Paleobotany: a sketch of the origin and evolution of floras. Ann. Rept., Smithson. Inst., (1918):289–407.

Bertrand, C.-E.

1874. Anatomie comparée des tiges et des feuilles chez les Gnetacées et les Conifères. Ann. Sci. Nat. Bot., sér. 5, 20:5–153.

1911. Le bourgeon femelle des Cordaites d'après les préparations de Bernard Renault. Bull. Soc. Sci. Nancy, pp. 1–61.

Bertrand, C.-E., and B. Renault

1884–1887. Recherches sur les Poroxylons. Archiv. Bot. du Nord France, 2:243–389.

1889. Les Poroxylons. Bulletin, Soc. Hist. Natur. d'Autun, 2:5–60.

Bertrand, P.

1947. Les végétaux vasculaires. 184 pp. Paris: Masson et cie.

Bertrand, P., and P. Corsin

1938. Phylogénie des végétaux vasculaires. Bull. Soc. Bot. France, 85:331–348, 503.

Boureau, E.

1939. Recherches anatomiques et expérimentales sur l'ontogénie des plantules des Pinacées et ses rapports avec la phylogénie. Ann. Sci. Nat. Bot., sér 11, 1: 1–219.

1949. Sur l'évolution de la ponctuation araucarienne dans les bois vivants et fossiles. Bull. Soc. Bot. France, 96:94–97.

1950. Le xylème centripète foliaire et la représentation graphique de l'accélération de l'appareil conducteur. Rev. Scient., 88:202–208.

1952. L'évolution des végétaux et l'anatomie des plantules. Ann. Biol., 28:C 163–191.

Bower, F. O.

1885. On the comparative morphology of the leaf in the vascular cryptogams and gymnosperms. Philos. Trans. Roy. Soc. London, B 175:565–615.

1890. On antithetic as distinct from homologous alternation of generations in plants. Ann. Bot., 4:347–370.

1894. A theory of the strobilus in archegoniate plants. Ann. Bot., 8:343–365.

BOWER, F. O. (Cont.)

1908. The Origin of a Land Flora. x + 727 pp. London: Macmillan and Co.

1929. The Origin of a Land Flora (1908–1929). Huxley Memorial Lecture 1929, Imp. Coll. Sci. and Tech., 27 pp. London: Macmillan and Co.

1930. Size and Form in Plants with Special Reference to the Primary Conducting Tracts. xiv + 232 pp. London: Macmillan and Co.

1935. Primitive Land Plants, also Known as the Archegoniatae. xiv + 658 pp. London: Macmillan and Co.

BRAUN, A.

1831. Vergleichende Untersuchung über die Ordnung der Schuppen an den Tannenzapfen. Nova Acta Leop. Carol., 15:195–402.

1835. Dr. Carl Schimper's Vorträge über die Möglichkeit eines wissenschaftlichen Verständnisses der Blattstellung Flora, 18(1):145–192.

1860. Über Polyembryonie und Keimung von Coelobogyne. Abh. K. Akad. Wiss. Berlin (1859), pp. 241–244.

1864. Uebersicht des natürlichen Systems nach der Anordnung desselben. *In* P. Ascherson, Flora der Provinz Brandenburg, der Altmark und des Herzogsthums Magdeburg, 1:22–67. Berlin: A. Hirschwald.

1876. Die Frage nach der Gymnospermie der Cycadeen erläutert durch die Stellung dieser Familie in Stufengang des Gewächreichs. Monatsber. K. Preuss. Akad. Wiss., 40:289–377.

BREBNER, G.

1902. On the anatomy of Danaea and other Marattiaceae. Ann. Bot., 16:517–552.

BRONGNIART, A.

1849. Tableau des genres de végétaux fossiles considérés sous le point de vue de leur classification botanique et de leur distribution géologique. 127 pp. Paris: L. Martinet.

1881. Recherches sur les graines fossiles silicifiés. xiv + 93 pp. Paris: G. Masson.

BROWN, R.

1825(1826). Character and description of *Kingia*, a new genus of plants found on the southwest coast of New Holland: with observations on the structure of its unimpregnated ovulum; and on the female flower of Cycadeae and Coniferae. *In* P. P. King, Narrative of a Survey of the Intertropical and Western Coasts of Australia, Performed between the Years 1818 and 1822, 2(app. B): 534–565. London: John Murray.

1844. On the plurality and development of the embryos in the seeds of Coniferae. Ann. and Mag. Nat. Hist., 13:368–374.

BUCHHOLZ, J. T.

1929. The embryogeny of the conifers. Proc. Internat. Cong. Plant Sci., Ithaca (1926), 1:359–392.

1933. Determinate cleavage polyembryony, with special reference to *Dacrydium*. Bot. Gaz., 94:579–588.

1934. The classification of Coniferales. Trans. Ill. Acad. Sci., 21:112–113.

BUCHHOLZ, J. T., and N. E. GREY

1948, 1951. A taxonomic revision of *Podocarpus*. I–VI. Journ. Arnold Arbor., 29:49–76, 117–151; 32:82–97.

BUGNON, P.

1922. L'origine phylogénique des plantes vasculaires d'après Lignier et la nouvelle classe des Psilophytales. Bull. Soc. Linn. Normandie, ser. 8, 4:196–212.

BURLINGAME, L. L.

1915a. The morphology of *Araucaria brasiliensis*. III. Fertilization, the embryo, and the seed. Bot. Gaz., 59:1–39.

1915b. The origin and relationships of the Araucarians. I–II. Bot. Gaz., 60:1–26, 89–114.

CAMPO-DUPLAN, M. VAN

1950. Recherches sur la phylogénie des Abiétinées d'après leurs grains de pollen. Trav. Labor. Forest. Toulouse, (tome 2[1]), 4(1):1–183.

1951. Recherches sur la phylogénie des Taxodiacées d'après leurs grains de pollen. Trav. Labor. Forest. Toulouse (tome 2[1]), 4(2):10–14.

CANDOLLÈ, A. P. DE

1813–1819. Théorie élémentaire de la botanique. 1st ed.: viii + 500 pp.; 2nd ed.: viii + 566 pp. Paris: Roret.

CARPENTIER, A.

1932. Étude de quelques végétaux jurassiques du Doubs. Mém. Soc. Géol. France, n.s., 8(1):1–12.

1937. Remarques sur les empreintes de *Frenelopsis* trouvées dans le Campanien inférieur du Massif de la Sainte-Baume. Ann. Mus. Hist. Nat. Marseille, 28(4): 1–14.

CARRUTHERS, W.

1870. On fossil Cycadean stems from the Secondary rocks of Britain. Trans. Linn. Soc. London, 26:675–708.

CASPARY, R.

1860. De Abietinearum Carr. flores feminei structura morphologica. Ann. Sci. Nat. Bot., sér. 4, 14:200–209.

ČELAKOVSKÝ, L.

1874. Ueber die verschiedenen Formen und die Bedeutung des Generationswechsels der Pflanzen. Sitzungsber. K. Böhm. Ges. Wiss., 16:21–61.

1879. Zur Gymnospermie der Coniferen. Flora, 62:257–264, 273–283.

1882a. Zur Kritik der Ansichten von der Fruchtschuppe der Abietineen, nebst einem morphologischen Excurse über die weiblichen Blüthen der Coniferen. Abh. K. Böhm. Ges. Wiss., math.-naturw. Kl., ser 6, 11:1–62.

1882b. Über Herrn A. W. Eichler's Entgegnung auf meine Kritik seiner Ansicht von der Fruchtschuppe der Abietineen. Sitzungsber. K. Böhm. Ges. Wiss., pp. 357–370.

1884. Untersuchungen über die Homologien der generativen Produkte der Fruchtblätter bei den Phanerogamen und Gefässkryptogamen. Jahrb. Wiss. Bot., 14:291–378.

1890. Die Gymnospermen. Eine morphologisch-phylogenetische Studie. Abh. K. Böhm. Geo. Wiss., math.-naturw. Kl., ser. 7, 4:1–148.

1898. Nachtrag zu meiner Schrift über die Gymnospermen. Bot. Jahrb., 24:202–231.

1900. Neue Beiträge zum Verständnis der Fruchtschuppe der Coniferen. Jahrb. Wiss. Bot., 35:407–448.

CHADEFAUD, M.

1940. La structure du carpelle chez les Conifères. Rev. Scient., 78:377–379.

1944. Les Préphanérogames. Rev. Scient., 82:244–246.

1949. Le sporophyte des plantes supérieures. Rev. Scient., 87:89–112.

Chamberlain, C. J.

1920. The living cycads and the phylogeny of seed plants. Amer. Journ. Bot., 7:146–153.

1935. Gymnosperms, Structure and Evolution. xi + 484 pp. Chicago: Univ. Chicago Press.

Chaney, R. W.

1951. A revision of fossil *Sequoia* and *Taxodium* in western North America based on the recent discovery of *Metasequoia*. Trans. Amer. Philos. Soc., n.s., 40:169–239.

Chauveaud, G.

1904. Origin secondaire du double faisceau foliaire chez les Sapins (*Abies*) et les Pins (*Pinus*). Ann. Sci. Nat. Bot., sér. 8, 19:335–348.

1912. Le type cycadéen et la phylogénie des Phanérogames. Bull. Soc. Bot. France, 59:694–703.

1921. La constitution des plantes vasculaires révélée par leur ontogénie. 155 pp. Paris: Payot et cie.

Chester, K. S.

1937. A critique of plant serology. Quart. Rev. Biol., 12:19–46, 165–190, 294–321.

Chodat, R.

1920. Principes de botanique. 3rd ed., ix + 878 pp. Genève: Atar.

Chrysler, M. A.

1932. A new cycadeoid from New Jersey. Amer. Jour. Bot., 19:679–692.

1937. Persistent juveniles among the cycads. Bot. Gaz., 98:696–710.

Church, A. H.

1914. On the floral mechanism of *Welwitschia mirabilis* Hooker. Philos. Trans. Roy. Soc. London, B 205:115–151.

Conard, H. S.

1919. The classification of vascular plants: a review. Plant World, 22:59–70.

Cookson, I. C., and S. L. Duigan

1951. Tertiary Araucariaceae from southeastern Australia, with notes on living species. Austral. Journ. Sci. Res., ser. B, 4:415–449.

Coulter, J. M., and C. J. Chamberlain

1917. Morphology of Gymnosperms. 2nd ed., xi + 466 pp. Chicago: Univ. Chicago Press.

Coulter, J. M., and W. J. G. Land

1905. Gametophytes and embryo of *Torreya taxifolia*. Bot. Gaz., 39:161–178.

Cranwell, L. M.

1941. Pollen grains of the New Zealand Conifers. New Zealand Journ. Sci. and Tech., 22(1 B):1–17.

Cribbs, J. E.

1938. A new fossil plant from the Reed Springs formation of southwestern Missouri. Amer. Journ. Bot., 25:311–321.

1939. *Cauloxylon ambiguum*, gen. et sp. nov., a new fossil plant from the Reed Springs formation of southwestern Missouri. Amer. Journ. Bot., 26:440–449.

1940. Structures of fossil stem of Pityean affinity from the Reed Springs formation of Missouri. Bot. Gaz., 101:582–597.

CROOKALL, R.

1930. *Crossotheca* and *Lyginopteris oldhamia*. Ann. Bot. London, 44:621–637.

DANSER, B. H.

1950. A theory of systematics. Bibl. Biotheor., 4:115–180.

DARLINGTON, C. D., and E. K. JANAKI AMMAL

1945. Chromosome Atlas of Cultivated Plants. 397 pp. London: George Allen & Unwin.

DARWIN, C.

1859. On the Origin of Species by Meaus of Natural Selection. ix + 502 pp. London: John Murray.

DELPINO, F.

1889. Applicazione di nuovi criterii per la classificazione della piante. II. Mem. R. Accad. Sci. Inst. Bologna, ser. 4, 10:43–75.

DLUHOSCH, H.

1937. Entwicklungsgeschichtliche Untersuchungen über die Mikrosporophyllgestaltung der Coniferen. Bibl. Bot., 114(3):1–20.

DOAK, C. C.

1932. Multiple male cells in *Cupressus arizonica*. Bot. Gaz., 94:168–182.

1935. Evolution of foliar types, dwarf shoots, and cone scales of *Pinus*, with remarks concerning similar structures in related forms. Ill. Bot. Monogr., 13:1–106.

DOYLE, J.

1926. Notes on the staminate cone of *Larix leptolepis*. Proc. Roy. Irish Acad., B 37: 154–169.

1945. Developmental lines in pollination mechanisms in the Coniferales. Sci. Proc. Roy. Dublin Soc., n.s., 24:43–62.

DOYLE, M. H., and J. DOYLE

1948. Pith structure in conifers. I. Taxodiaceae. Proc. Roy. Irish Acad., B 52:15–39.

DOYLE, J., and W. J. LOOBY

1939. Embryogeny in *Saxegothaea* and its relation to other podocarps. Sci. Proc. Roy. Dublin Soc., n.s., 22:127–147.

DOYLE, J., and M. O'LEARY

1934. Abnormal cones of *Fitzroya* and their bearing on the nature of the Conifer strobilus. Sci. Proc. Roy. Dublin Soc., n.s., 21:23–35.

DUPLER, A. W.

1919. Staminate strobilus of *Taxus canadensis*. Bot. Gaz., 68:345–366.

1920. Ovuliferous structures of *Taxus canadensis*. Bot. Gaz., 69:492–520.

EAMES, A. J.

1913. The morphology of *Agathis australis*. Ann. Bot., 27:1–38.

1936. Morphology of Vascular Plants: Lower Groups (Psilophytales to Filicales). xviii + 433 pp. New York and London: McGraw-Hill.

1951. Again: "The New Morphology." New Phytol., 50:17–35.

1952. Relationships of the Ephedrales. Phytomorphology, 2:79–100.

EAMES, A. J., and L. H. MACDANIELS

1925–1947. An Introduction to Plant Anatomy. 1st ed., xiv + 364 pp.; 2nd ed., xvii + 427 pp. New York: McGraw-Hill.

ECKHOLD, W.

1922. Die Hoftüpfel bei rezenten und fossilen Coniferen. Jahrb. Preuss. Geol. Landesanst., 42:472–505.

Eichler, A. W.

1863. Excursus morphologicus de formatione florum Gymnospermarum. Ann. Sci. Nat. Bot., sér. 4, 19:257–285.

1875. Blüthendiagramme. Erster Theil. viii + 347 pp. Leipzig: W. Engelmann.

1880. Syllabus der Vorlesungen über specielle und medicinischpharmaceutische Botanik. iv + 47 pp. Berlin: Gebr. Borntraeger.

1881. Über die weiblichen Blüthen der Coniferen. Monatsber. K. Preuss. Akad. Wiss., pp. 1–32.

1882a. Über Bildungsabweichungen bei Fichtenzapfen. Sitzungsber. K. Preuss. Akad. Wiss., phys.-math. Kl., pp. 25–42.

1882b. Entgegnung auf Herrn L. Čelakovský's Kritik meiner Ansicht über die Fruchtschuppe der Abietineen. Sitzungsber. Ges. Naturforsch. Freunde zu Berlin, pp. 79–92.

Emberger, L.

1944. Les plantes fossiles dans leurs rapports avec les végétaux vivants. 492 pp. Paris: Masson et cie.

1949. Les Préphanérogames. Ann. Sci. Nat. Bot. et Biol. végétale, sér. 11, 10:131–144.

1950. La valeur morphologique et l'origine de la fleur. Ann. Biol., 26:279–296.

1952a. Tige, racine, feuille. Ann. Biol., 28:C 109–128.

1952b. Encore sur les Préphanérogames avec remarques générales sur la systématique. Rec. Trav. Labor. Bot. Géol. et Zool. Fac. Sci., Univ. Montpellier, sér. Bot. No. 5, pp. 11–14.

Endlicher, S.

1847. Synopsis Coniferarum. iv + 368 pp. Sangalli: Scheitlin u. Zollikofer.

Engler, A.

1892. Syllabus der Vorlesungen über specielle und medizinischpharmaceutische Botanik. xxiii + 184 pp. Berlin: Gebr. Borntraeger.

Engler, A., and L. Diels

1936. Syllabus der Pflanzenfamilien. 11th ed., xliii + 419 pp. Berlin: Gebr. Borntraeger.

Engler, A., and E. Gilg

1924. Syllabus der Pflanzenfamilien. 9th and 10th eds., xliii + 420 pp. Berlin: Gebr. Borntraeger.

Engler, A., and K. Prantl

1889. Die natürlichen Pflanzenfamilien. Teil II:1. 262 pp. Leipzig: W. Engelmann.

1897. Die natürlichen Pflanzenfamilien. Nachträge zum II–IV Teil. 380 pp. Leipzig: W. Engelmann.

Erdtman, H.

1952. Chemistry of some heartwood constituents of conifers and their physiological and taxonomic significance. *In* Progress in Organic Chemistry, pp. 22–63. London: Butterworths Sci. Publs.

Esau, K.

1939–1950. Development and structure of the phloem tissue. I–II. Bot. Rev., 5:373–432; 16:67–114.

1943. Origin and development of primary vascular tissues in seed plants. Bot. Rev., 9:125–206.

Fagerlind, F.

1941. Bau und Entwicklung der Gnetum-Gametophyten. Handl. K. Sv. Vet.-Akad., ser. 3, 19(8):1–55.

FAGERLIND, F. (Cont.)

1946. Strobilus und Blüte von *Gnetum* und die Möglichkeit, aus ihrer Struktur den Blütenbau der Angiospermen zu deuten. Arkiv Bot. K. Sv. Vet.-Akad., 33 A (8):1–57.

FAVRE-DUCHARTRE, M.

1943. Sur le comportement des ovules de *Ginkgo biloba*. Bull. Soc. Bot. France, 90:111–116.

FERNANDES, A.

1936. Sur la caryologie de *Welwitschia mirabilis* Hook. f. Bol. Soc. Brot., 11(II): 267–282.

FERRÉ, Y. DE

1939. Cotylédons et évolution chez les Abiétinées. Bull. Soc. Hist. Nat. Toulouse, 73:299–314.

1942. A'propos des cotylédons des Abiétinées. Bull. Soc. Hist. Nat. Toulouse, 77:56–60.

1943. L'évolution parallèle des Taxodinées et des Abiétinées. Bull. Soc. Hist. Nat. Toulouse, 78:71–83.

1952. La signification des formes de jeunesse dans l'étude de l'évolution. Ann. Biol., 28:C 193–205.

FERRÉ, Y. DE, and H. GAUSSEN

1945. Le rameau phylétique: *Pinus, Pseudolarix, Keteleeria*. Bull. Soc. Hist. Nat. Toulouse, 80:108–118.

FLORIN, R.

1931. Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. I. Morphologie und Epidermisstruktur der Assimilationsorgane bei den rezenten Koniferen. Handl. K. Sv. Vet.-Akad., ser. 3, 10:1–588.

1932. Die Chromosomenzahlen bei *Welwitschia* und einigen *Ephedra*-Arten. Svensk Bot. Tidskr., 26:205–214.

1933. Studien über die Cycadales des Mesozoikums nebst Erörterungen über die Spaltöffnungsapparate der Bennettitales. Handl. K. Sv. Vet.-Akad., ser. 3, 12(5):1–134.

1934. Die Spaltöffnungsapparate von *Welwitschia mirabilis* Hook. f. Svensk Bot. Tidskr., 28:264–289.

1936a. Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters. Palaeontographica, B 81:71–173; B 82:1–72.

1936b. On the structure of the pollen-grains in the Cordaitales. Svensk Bot. Tidskr., 30:624–651.

1937. On the morphology of the pollen-grains in some Palaeozoic pteridosperms. Svensk Bot. Tidskr., 31:305–338.

1938–1945. Die Koniferen des Oberkarbons und des unteren Perms. I–VIII. Palaeontographica, B 85:1–729.

1940a. On *Walkomia* (=*Walkomiella*) n. gen., a genus of Upper Palaeozoic Conifers from Gondwanaland. Handl. K. Sv. Vet.-Akad., ser. 3, 18(5):1–23.

1940b. The Tertiary fossil conifers of South Chile and their phytogeographical significance, with a review of the fossil conifers of southern lands. Handl. K. Sv. Vet.-Akad., ser. 3, 19(2):1–107.

1948a. On the morphology and relationships of the Taxaceae. Bot. Gaz., 110:31–39.

1948b. On *Nothotaxus*, a new genus of the Taxaceae, from eastern China. Acta Hort. Berg., 14:385–395.

1949. The morphogy of *Trichopitys heteromorpha Saporta*, a seed-plant of Palaeozoic age, and the evolution of the female flowers in the Ginkgoinae. Acta Hort. Berg., 15:79–109.

FLORIN, R. (Cont.)

1951. Evolution in cordaites and conifers. Acta Hort. Berg., 15:285–388.

1952a. On *Metasequoia*, living and fossil. Bot. Not., pp. 1–29.

1952b. Evolution et classification des Gymnospermes. Ann. Biol., 28:C 99–108.

FLORY, W. S.

1936. Chromosome numbers and phylogeny in the gymnosperms. Journ. Arnold Arbor., 17:83–89.

FLOUS, F.

1936a. Classification et évolution d'un groupe d'Abiétinées. Trav. Labor. Forest. Toulouse, (tome 1), 2(17):1–286.

1936b. Évolution des rameaux chez les Pinacées. Bull. Soc. Hist. Nat. Toulouse, 69: 95–102.

1938a. Signification des rameaux et bourgeons de cèdre. Bull. Soc. Hist. Nat. Toulouse, 72:99–124.

1938b. A'propos de l'évolution des Abiétinées. Bull. Soc. Hist. Nat. Toulouse, 72:829–304.

FOSTER, A. S.

1939. Problems of structure, growth and evolution in the shoot apex of seed plants. Bot. Rev., 5:454–470.

1941. Comparative studies on the structure of the shoot apex in seed plants. Bull. Torrey Bot. Club, 68:339–350.

1949. Practical Plant Anatomy. 2nd ed., xi + 228 pp. New York: D. Van Nostrand Co.

FRAINE, E. DE

1912. On the structure and affinities of *Sutcliffia*, in the light of a newly discovered specimen. Ann. Bot., 26:1031–1066.

FRENTZEN, K.

1931. Studien über die fossilen Hölzer der Sammelgattung *Dadoxylon* Endl. I–II. Abh. Heidelberg. Akad. Wiss., 16:1–93; 19:1–51.

GAUSSEN, H.

1941–1952. Les Gymnospermes actuelles et fossiles. I–VIII. Trav. Labor. Forest. Toulouse, (tome 2, sec. 1), 1(1):1–72; 1(2):1–40; 1(3):1–104; 1(4):1–43; 1(5):1–26; 1(6):1–24; 1(7):1–54; 1(8):1–248.

1948. Interprétation de l'écaille du cône chez les Conifères. Compt. Rend. Acad. Sci. Paris, 227:731–733.

1952. L'évolution pseudocyclique. Ann. Biol., 28:C 207–225.

GEYLER, T.

1867–1868. Ueber den Gefässbündelverlauf in den Laubblattregionen der Coniferen. Jahr. Wiss. Bot., 6:55–208.

GIBBS, R. D.

1945. Comparative chemistry as an aid to the solution of problems in systematic botany. Trans. Roy. Soc. Canada, ser. 3, 36(sec. 5):71–103.

GILG, E., and P. N. SCHÜRHOFF

1927. Unsere Erfahrungen über die Brauchbarkeit der Serodiagnostik für die botanische Verwandtschaftsforschung. Ber. Deutch. Bot. Ges., 45:315–330, 602–606.

GOEBEL, K.

1923. Organographie der Pflanzen. 1st ed., 3(2):1493–1789. Jena: G. Fischer.

1932. Organographie der Pflanzen. 2nd ed., 3(1):i–viii, 1379–1820. Jena: G. Fischer.

GOEPPERT, H. R.

1850. Monographie der fossilen Coniferen. Natur. Verh. Hollandsche Maatschappij der Wetenschappen, Tweede Verzameling, pt. 2., pp. i–ix, 1–286, 1–72.

GOEPPERT, H. R., and G. STENZEL

1881. Die Medulloseae. Eine neue Gruppe der fossilen Cycadeen. Palaeontographica, n.s., 8(3):113–127.

GORDON, W. T.

1935. The genus *Pitys*, Witham, emend. Trans. Roy. Soc. Edinburgh, 58(2):279–311.

1938. On *Tetrastichia bupatides:* a Carboniferous Pteridosperm from East Lothian. Trans. Roy. Soc. Edinburgh, 59(2):351–370.

1941. On *Salpingostoma dasu:* a new Carboniferous seed from East Lothian. Trans. Roy. Soc. Edinburgh, 60(2):427–464.

GOTHAN, W.

1905. Zur Anatomie lebender und fossiler Gymnospermen-Hölzer. Abh. K. Preuss. Geol. Landesanst., n.s., 44:1–108.

GRAMBAST, L.

1951. *Tetraclinoxylon* (*Cupressionoxylon* p.p.) *Boureaui* nov. gen., nov. spec. Bois fossile du Chattien du Bassin de Paris. Bull. Soc. Géol. France, sér. 6, 1:227–284.

GRAND'EURY, F. C.

1877. Mémoire sur la flore carbonifère du Départment de la Loire et du Centre de la France. Mém. Acad. Sci. Inst. Nat. France, 24(1):1–624.

1905. Sur les graines trouvées attachées au *Pecopteris Pluckeneti* Schlot. Compt. Rend. Acad. Sci. Paris, 140:920–923.

GREGUSS, P.

1950. Xylotomischer Bestimmungsschlüssel der heute lebenden Koniferen-Gattungen. Acta Biol. Acad. Sci. Hungar., 1:207–327.

1951. Xylotomischer Bestimmungsschlüssel der Gattungen und Arten der Podocarpaceae. Acta Biol. Acad. Sci. Hungar., 3:53–149.

GREY, N. E., and J. T. BUCHHOLZ. *See* Buchholz and Grey

GRIFFITH, M. M.

1952. The structure and growth of the shoot apex in *Araucaria*. Amer. Journ. Bot., 39:253–263.

GUNCKEL, J. E., and R. H. WETMORE

1946. Studies of development in long shoots and short shoots of *Ginkgo biloba* L. I. The origin and pattern of development of the cortex, pith and procambium. II. Phyllotaxis and the organization of the primary vascular system: primary phloem and primary xylem. Amer. Journ. Bot., 33:285–295, 532–543.

HAAN, H. R. M. DE

1920. Contribution to the knowledge of the morphological value and the phylogeny of the ovule and its integuments. Rec. Trav. Bot., Néerl., 17:219–324.

HAGERUP, O.

1933. Zur Organogenie und Phylogenie der Koniferen-Zapfen. K. Dansk. Vidensk. Selsk., Biol. Meddel., 10(7):1–82.

1934. Zur Abstammung einiger Angiospermen durch Gnetales und Coniferae. K. Danske Vidensk. Selsk., Biol. Meddel., 11(4):1–83.

HALKET, A. C.

1930. The rootlets of "Amyelon radicans" Will., their anatomy, their apices, and their endophytic fungus. Ann. Bot., 44:865–905.

1932. A note on the origin of lateral roots and the structure of the root-apex of *Lyginopteris oldhamia*. New Phytol., 31:279–283.

HALLE, T. G.

1929. Some seed-bearing pteridosperms from the Permian of China. Handl. K. Sv. Vet.-Akad., ser. 3, 6(8):1–24.

1933. The structure of certain fossil spore-bearing organs believed to belong to pteridosperms. Handl. K. Sv. Vet.-Akad., ser. 3, 12(6):1–103.

1937. The position and arrangement of the spore-producing members of the Palaeozoic pteridosperms. Compt. Rend. 2ème Congr. Stratigr. Carbon. (Heerlen, 1935), pp. 227–235.

1938–1940. De utdöda växterna. I–II. *In* Växternas liv, C. Skottsberg, ed., 4:449–667; 5:1–136. Stockholm: Nordisk Familjeboks Fölagsaktiebolag.

HANSTEIN, J.

1868. Die Scheitelzellgruppe im Vegetationspunkt der Phanerogamen. Festschrift, Niederrhein. Ges. Natur- u. Heilkunde zum 50 jährigen Jubiläum Univ. Bonn, pp. 1–26. Bonn.

HARRIS, T. M.

1932–1937. The fossil flora of Scoresby Sound, East Greenland. 2–5. Meddelel. om Grönland, 85(3):1–114; 85(5):1–133; 112(1):1–176; 112(2):1–114.

1933. A new member of the Caytoniales. New Phytol., 32:97–114.

1940a. On *Caytonia* Thomas. Ann. Bot., n.s., 4:713–734.

1940b. On some Jurassic specimens of *Sagenopteris*. Ann. and Mag. Nat. Hist., ser. 11, 6:249–265.

1941a. Cones of extinct Cycadales from the Jurassic rocks of Yorkshire. Philos. Trans. Roy. Soc. London, B 231:75–98.

1941b. *Caytonanthus*, the microsporophyll of *Caytonia*. Ann. Bot., n.s., 5:47–58.

1942–1952. Notes on the Jurassic flora of Yorkshire, 1–12, 14–17, 20–25, 27–31, 33, 36, 38–47, 49–57. Ann. and Mag. Nat. Hist., Ser. 11—9:568–587; 10:506–522, 837–854; 11:419–433, 674–690; 12:213–222, 366–378, 475–488, 820–82,5 829–835; 13:1–24, 392–400, 407–411, 659–662. Ser. 12—1:192–213; 2:275–299, 561–585; 3:1001–1020; 4:915–937; 5:362–382, 614–627.

1943. The fossil conifer *Elatides Williamsoni*. Ann. Bot., n.s., 7:325–339.

1944. A revision of *Williamsoniella*. Philos. Trans. Roy. Soc. London, B 231:313–328.

1947. The problems of Jurassic palaeobotany. Bol. Soc. Geol. Portugal, 6(3):1–32.

1951a. The relationships of the Caytoniales. Phytomorphology, 1:29–39.

1951b. The fructification of *Czekanowskia* and its allies. Philos. Trans. Roy. Soc. London, B 235:483–508.

HERZFELD, S.

1914. Die weibliche Koniferenblüte. Oesterr. Bot. Zeitschr., 64:321–358.

HIITONEN, I.

1950. Ein neuer Fall von Zapfensucht bei der Kiefer, *Pinus silvestris* L., und wie ein solcher zu erklären ist. Mem. Soc. Fauna et Flora Fenn., 25:115–120.

HILL, T. G., and E. DE FRAINE

1913. A consideration of the facts relating to the structure of seedlings. Ann. Bot., 27:257–272.

HIRASE, S.

1895, 1898. Études sur la fécondation et l'embryogénie du *Ginkgo biloba*. I, II. Journ. Coll. Sci. Imp. Univ. Tokyo, 8:307–322; 12:103–149.

HIRMER, M.

1932. Zur Kenntnis der strukturbietenden Pflanzenreste des jüngeren Paläozoikums. 1. Über einen fertilen Spross von Cordiaten-Verwandtschaft: *Gothamia westfalica* nov. gen. u. spec. Palaeontographica, 77:121–140.

1936. Entwicklungsgeschichte und vergleichende Morphologie des weiblichen Blütenzapfens der Coniferen. Bibl. Bot., 114(1):1–100.

1937. Die Pteridospermae, insbesondere die Caytoniales, und die Entwickelung der Angiospermae. Compt. Rend. 2ème Congr. Stratigr. Carbon. (Heerlen, 1935), pp. 271–289.

1941. Paläobotanik. Fortschr. Bot., 10:56–112.

HIRMER, M., and L. HÖRHAMMER

1934. Zur weiteren Kenntnis von *Cheirolepis* Schimper und *Hirmeriella* Hörhammer mit Bemerkungen über deren systematische Stellung. Palaeontographica, B 79:67–84.

HOFMEISTER, W.

1849. Die Entstehung des Embryo der Phanerogamen. v + 89 pp. Leipzig: Fr. Hofmeister.

1851. Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen (Moose, Farrn, Equisetaceen, Rhizocarpeen und Lycopodiaceen) und der Samenbildung der Coniferen. viii + 179 pp. Leipzig: Fr. Hofmeister.

1858. Neuere Beobachtungen über Embryobildung der Phanerogamen. Jahrb. Wissens. Bot., 1:82–188.

1867. Die Lehre von der Pflanzenzelle. *In* W. Hofmeister, Handbuch der physiologischen Botanik, 1:1–404. Leipzig: W. Engelmann.

1868. Allgemeine Morphologie der Gewächse. *In* W. Hofmeister, Handbuch der physiologischen Botanik, 1:405–664. Leipzig: W. Engelmann.

HOLLICK, A., and E. C. JEFFREY

1909. Studies of Cretaceous coniferous remains from Kreischerville, New York. Mem. New York Bot. Gard., 3:1–138.

HOLLOWAY, J. T.

1938. On the phylogenetic significance of the diterpenes of the phyllocladene and podocarprene groups. N. Zealand Journ. Sci. and Tech., 20(B):16–20.

HOLTHUSEN, K.

1940. Untersuchungen über das Vorkommen und den Zustand der Achselknospen bei den höheren Pflanzen. Planta, 30:590–638.

HÖRHAMMER, L.

1933. Über die Coniferen-Gattungen *Cheirolepis* Schimper und *Hirmeriella* nov. gen. aus dem Rhät-Lias von Franken. Bibl. Bot., 107:1–34.

HOSKINS, J. H., and A. T. CROSS

1946. Studies in the Trigonocarpales. I–II. Amer. Midl. Nat., 36:207–250, 331–361.

HU, H. H., and W.-C. CHENG

1948. On the new family Metasequoiaceae and on *Metasequoia glyptostroboides*, a living species of the genus *Metasequoia* found in Szechuan and Hupeh. Bull. Fan Memor. Inst. Biol., n.s., 1:153–161.

HUBER, B.

1948. Zur Mikrotopographie der Saftströme im Transfusionsgewebe der Koniferennadel. I. Anatomischer Teil. Planta, 35:331–351.

HUTCHINSON, J.

1924. Contributions towards a phylogenetic classification of flowering plants. III. The genera of gymnosperms. Kew Bull., pp. 19–66.

Huxley, J.

1940. The New Systematics. viii + 583 pp. Oxford: Clarendon Press.

Ikeno, S.

1898. Untersuchungen über die Entwicklung der Geschlechtsorgane und den Vorgang der Befruchtung bei *Cycas revoluta*. Journ. Coll. Sci. Imp. Univ. Tokyo, 12:151–214.

International Association of Wood Anatomists, Committee on Nomenclature

1933. Glossary of terms used in describing woods. Trop. Woods, no. 36, pp. 1–12.

Janchen, E.

1949. Das System der Koniferen. Sitzungsber. Oesterr. Akad. Wiss., math.-naturw. Kl. (div. 1), 158:155–262.

Jeffrey, E. C.

1899a. The development, structure, and affinities of the genus *Equisetum*. Mem. Boston Soc. Nat. Hist., 5:155–190.

1899b. The morphology of the central cylinder in the angiosperms. Trans. Canad. Inst., 6:599–636.

1902. The structure and development of the stem in the Pteridophyta and gymnosperms. Philos. Trans. Roy. Soc. London, B 195:119–146.

1908. On the structure of the leaf in Cretaceous pines. Ann. Bot., 22:593–602.

1910. The Pteropsida. Bot. Gaz., 50:401–414.

1912. The history, comparative anatomy and evolution of the *Araucarioxylon* type. Proc. Amer. Acad., 48:531–549, 551–561, 563–571.

1917. The Anatomy of Woody Plants. x + 478 pp. Chicago: Univ. Chicago Press.

1925. The origin of parenchyma in geological time. Proc. Nat. Acad. Sci. Washington, 11:106–110.

Jeffrey, E. C., and R. E. Torrey

1916. *Ginkgo* and the microsporangial mechanisms of the seed plants. Bot. Gaz., 62:281–292.

Jensen, H., and A. Levan

1941. Colchicine-induced tetraploidy in *Sequoia gigantea*. Hereditas, Vols. 220–224.

Johansen, D. A.

1950. Plant Embryology. Embryogeny of the Spermatophyta. xviii + 305 pp. Waltham, Mass.: Chronica Botanica Co.

1951. A modern classification of the plant kingdom. Biologia (Chron. Bot.), 2:200–201.

Johnson, M. A.

1951. The shoot apex in gymnosperms. Phytomorphology, 1:188–204.

Juel, H. O.

1900. Beiträge zur Kenntniss der Tetradenteilung. Jahrb. Wiss. Bot., 35:626–659.

1904. Über den Pollenschlauch von *Cupressus*. Flora, 93:56–62.

Karstens, W. K. H.

1945. Variability of the female reproductive organs in *Ginkgo biloba* L. Blumea, 5: 532–553.

Kershaw, E. M.

1912. Structure and development of the ovule of *Bowenia spectabilis*. Ann. Bot., 26:625–646.

Kidston, R.

1904. On the fructification of *Neuropteris heterophylla* Brongniart. Philos. Trans. Roy. Soc. London, B 197:1–5.

KIDSTON, R. (Cont.)

1923–1925. Fossil plants of the Carboniferous rocks of Great Britain, 2(4–6):276–681. London: E. Stanford.

KIDSTON, R., and W. J. JONGMANS

1911. Sur la fructification de *Neuropteris obliqua* Bgt. Arch. Néerl. Sci. Exact. et Nat., ser. III B, 1:25–26.

KIDSTON, R., and W. H. LANG

1921. On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. IV. Trans. Roy. Soc. Edinburgh, 52:831–854.

KIELLANDER, C. L.

1950. Polyploidy in *Picea Abies*. Hereditas, 36:513–516.

KIRCHHEIMER, F.

1950. Das Vorkommen von *Sciadopitys* im mitteleuropäischen Tertiär und die Bedeutung ihres Pollens für die Stratigraphie der Braunkohlenschichten. Neues Jahrb. Geol. u. Paläontol. Montash., pp. 59–64.

KOCH, L.

1891. Ueber Bau und Wachsthum der Sprosspitze der Phanerogamen. I. Die Gymnospermen. Jahrb. Wiss. Bot., 22:491–680.

KON'NO, E.

1944. Contribution to our knowledge of Swedenborgia. Jap. Journ. Geol. and Geog., 19:27–66.

KÖTTER, W.

1931. Normale und anomale Fruchtbildung bei *Juniperus communis*. Inaugural Diss. Univ. Hamburg, pp. 1–78.

KRAUS, G.

1870–1872. Bois fossiles de Conifères. *In* W. P. Schimper, Traité de paléontologie végétale, 2:363–385. Paris: J. B. Ballière et Fils.

1886. Beiträge zur Kenntniss fossiler Hölzer. II. Zur Diagnostik des Coniferenholzes. Abhandl. Naturforsch. Ges., Halle, 16:92–109.

KRÄUSEL, R.

1919. Die fossilen Koniferenhölzer (unter Ausschluss von *Araucarioxylon* Kraus). Palaeontographica, 62:185–275.

1938. Die Windsheimer Ähren. Ein Beitrag zur Kenntnis der Koniferen des süddeutschen Mesozoikums. Palaeontographica, B 84:21–44.

1943a. Die Ginkgophyten der Trias von Lunz in Nieder-österreich und von Neue Welt bei Basel. Untersuchungen zur mesozoischen Florengeschichte des alpinen und süddeutschen Raumes. II. Palaeontographica, B 87:59–93.

1943b. *Furcifolium longifolium* n. comb., eine Ginkgophyte aus dem Solnhofener Jura. Senckenbergiana, 26:426–433.

1948. *Sturiella langeri* nov. gen. nov. spec., eine Bennettitacee aus der Trias von Lunz (Nieder-österreich). Senckenbergiana, 29:141–149.

1949a. Koniferen und andere Gymnospermen aus der Trias von Lunz, Nieder-österreich. Untersuchungen zur mesozoischen Florengeschichte des alpinen und süddeutschen Raumes. III. Palaeontographica, B 89:35–82.

1949b. Die fossilen Koniferenhölzer (unter Ausschluss von *Araucarioxylon* Kraus). II. Kritische Untersuchungen zur Diagnostik lebender und fossiler Koniferen-Hölzer. Palaeontographica, B 89, 83–203.

1952. *Pachylepis* nov. gen., eine neue Koniferen-Gattung aus dem süddeutschen Keuper. Senckenbergiana, 32:343–350.

Kujala, V.

1942. Über die morphologische Deutung des Fichtenzapfens auf Grund eines Fertilisationsfalles. Acta Forest. Fennica, 50(7):1–22.

Lam, H. J.

1948. Classification and the new morphology. Acta Biotheor., 8:107–154.

1952. L'évolution des plantes vasculaires. Ann. Biol., 28:C 58–88.

Lanfer, K. F.

1933. Ein Beitrag zur Kenntnis der weiblichen Blüten der Coniferen. Ontogenetische und teratologische Untersuchungen über die weiblichen Blütenzapfen der Abietineen, der Cupressineen und der Taxaceen mit besonderer Berücksichtigung der bei einigen Arten vorkommenden Vergrünungen (Anamorphosen). Bot. Jahrb., 65:509–558.

1934. Beitrag zur Klärung und zum richtigen Verständnis der ontogenetischen Untersuchungen der Coniferen-Zapfen von O. Hagerup. Bot. Jahrb., 66:471–486.

Lang, W. H.

1900. Studies in the development and morphology of Cycadean sporangia. II. The ovule of *Stangeria paradoxa*. Ann. Bot., 14:281–306.

Langdon, L. D.-M.

1920. Stem anatomy of *Dioon spinulosum*. Bot. Gaz., 70:110–125.

Lavier-George, L.

1935. Les affinités des Gnétales. Bull. Sci. Bourgogne, 4:29–34.

Lawrence, G. H. M.

1951. Taxonomy of Vascular Plants. xiii + 823 pp. New York: Macmillan and Co.

Leclercq, S.

1928. Les végétaux à structure conservée du houiller Belge. Note 1. Feuilles et racines de Cordaitales des coal-balls de la Couche Bouxharmont. Ann. Soc. Géol. Belgique, 51(Bull.):1–14.

Li, H.-L.

1953. A reclassification of *Libocedrus* and Cupressaceae. Journ. Arnold Arbor., 34: 17–34.

Li, T.-L.

1934. The development of embryo of *Ginkgo biloba*. Sci. Repts. Nat. Tsing Hua Univ., B 2:29–35.

Lignier, O.

1894. Végétaux fossiles de Normandie. Structure et affinités du *Bennettites Morierei* Sap. et Mar. Mém. Soc. Linn. Normandie, 18:1–78.

1908–1909. Essai sur l'évolution morphologique du règne végétal. Bull. Soc. Linn. Normandie, sér. 6, 3:35–62.

Lignier, O., and A. Tison

1912. Les Gnetales, leurs fleurs et leur position systématique. Ann. Sci. Nat. Bot., sér. 9, 16:55–185.

1913. L'ovule tritégumenté des *Gnetum* est probablement un axe d'inflorescence. Bull. Soc. Bot. France, 60:64–72.

Lindstedt, G.

1951. Constituents of pine heartwood. XXVI. A general discussion. Acta Chem. Scandinavica, 5:129–138.

LOTSY, J. P.

1899. Contributions to the life-history of the genus *Gnetum*. I. The grosser morphology of reproduction in *Gnetum Gnemon*. Ann. Jard. Bot. Buitenzorg, sér. 2, 1:46–114.

1911. Vorträge über botanische Stammesgeschichte. III. 1055 pp. Jena: G. Fischer.

LOUBIÈRE, A.

1929. Étude anatomique et comparée du *Leptotesta* Grand'Euryi n. gen., n. sp. (graine silicifié du *Pecopteris Pluckeneti* Schlotheim). Rev. Gén. Bot., 41: 593–605.

1938. Recherches sur l'anatomie comparée des graines de Ptéridospermes. Arch. Mus. Hist. Nat. Paris, sér. 6, 15:23–57.

MCLEAN, R. C., and W. R. IVIMEY-COOK

1951. Textbook of Theoretical Botany, Vol. I. xv + 1069 pp. London: Longmans, Green and Co.

MCNAB, W. R.

1873. On the development of the flowers of *Welwitschia mirabilis* Hook. fil. Trans. Linn. Soc. London, 28:507–512.

MÄDLER, K.

1939. Die pliozäne Flora von Frankfurt am Main. Abh. Senckenberg. Naturforsch. Ges., no. 446, pp. 1–202.

MÄGDEFRAU, K.

1942. Paläobiologie der Pflanzen. vii + 396 pp. Jena: G. Fischer.

MANGENOT, G.

1952. L'évolution de l'ovule, du pistil et du fruit. Ann. Biol., 28:C 149–162.

MARKGRAF, F.

1926. Gnetales. *In* A. Engler, Die natürlichen Pflanzenfamilien. 2nd ed., 13:407–441. Leipzig: W. Engelmann.

MARTENS, P.

1948. La graine et le tube pollinique; réflexions sur les caractères propres des phanérogames. Bull. Acad. Roy. Belgique Sci., sér. 5, 33:919–943.

1951. Les Préphanérogames et le problème de la graine. Cellule, 54:105–132.

MASLEN, A. J.

1930. The structure of *Mesoxylon platypodium* and Mesoxyloides. Ann. Bot., 44: 503–533.

MATTE, H.

1904. Recherches sur l'appareil libéro-ligneux des Cycadacées. Mém. Soc. Linn. Normandie, 22:1–233.

MAYR, E.

1949. Systematics and the Origin of Species. xiv + 334 pp. New York: Columbia Univ. Press.

MEHRA, P. N.

1939. Some abnormalities in the female strobilus of *Ginkgo biloba* L. Proc. Indian Acad. Sci., 8(B):211–217.

1947. A study of the karyotypes and the occurrence of diploid male gametophytes in some species of the genus *Ephedra*. Proc. Nat. Acad. Sci. India, B 16: 259–286.

MESSERI, A.

1932. Il valore ontogenetico e filogenetico del legno centripeto foliare delle Cycadinae. Nuovo Giorn. Bot. Ital., n.s., 39:70–75.

METTENIUS, G.

1860. Beiträge zur Anatomie der Cycadeen. Abh. K. Sächs. Ges. Wiss., math-naturw. Kl., 7:565–608.

MEYER, F. J.

1917. Die Stelärtheorie und die neuere Nomenklatur zur Beschreibung der Wasserleitungsbahnen der Pflanzen. Beih. Bot. Centr., 33(1):129–168.

MEZ, C.

1926. Die Bedeutung der Sero-Diagnostik für die stammesgeschichtliche Forschung. Bot. Archiv., 16:1–23.

MIKI, S.

1941. On the change of flora in eastern Asia since Tertiary period. I. The clay or lignite beds flora in Japan with special reference to the *Pinus trifolia* beds in Central Hondo. Jap. Journ. Geol. and Geog., 11:237–303.

MIQUEL, F. A. W.

1869. On the sexual organs of the Cycadaceae. Journ. Bot., 7:64–78, 93–104.

MIROV, N. T.

1948. The terpenes (in relation to the biology of genus *Pinus*). Ann. Rev. Biochem., 17:521–540.

MITRA, A. K.

1927. On the occurrence of two ovules on Araucarian cone-scales. Ann. Bot., 41: 461–471.

MOHL, H. VON

1833. Einige Bemerkungen über die Entwicklung und den Bau cryptogamischer Gewächse. I. Flora, 16(1):33–46, 49–63, 65–78.

1845. Vermischte Schriften botanischen Inhalts. viii + 442 pp. Tübingen: L. F. Fues.

1851. Grundzüge der Anatomie und Physiologie der vegetabilischen Zelle. 152 pp. Braunschweig: Vieweg.

1853. Über die Zusammensetzung der Zellmembran. Bot. Zeit., 11:753–762, 769–775.

1871. Morphologische Betrachtung der Blätter von *Sciadopitys*. Bot. Zeit., 29:1–14, 17–26.

MOLISCH, H.

1933. Pflanzenchemie und Pflanzenverwandtschaft. viii + 118 pp. Jena: G. Fischer.

MORLEY, T.

1948. On leaf arrangement in *Metasequoia glyptostroboides*. Proc. Nat. Acad. Sci., Washington, 34:574–578.

MÜLLER-STOLL, W. R.

1948. Zytomorphologische Studien am Pollen von *Taxus baccata* L. und anderen Koniferen. Planta, 35:601–641.

NÄGELI, C. VON

1844–1846. Zellenkerne, Zellenbildung und Zellenwachsthum bei den Pflanzen, I-II. Zeitschr. Wiss. Bot., 1(1):34–133; 1(3):22–93.

1858. Ueber das Wachsthum des Stammes und der Wurzel bei den Gerfässpflanzen In C. von Nägeli, Beiträge zur wissenschaftlichen Botanik, 1:58–61. Leipzig: W. Engelmann.

1878. Ueber das Scheitelwachsthum der Phanerogamen. Bot. Zeit., 36:124–126.

NATHORST, A. G.

1902. Beiträge zur Kenntnis einiger mesozoischen Cycadophyten. Handl. K. Sv. Vet.-Akad., 36(4):1–28.

1908. Paläobotanische Mitteilungen. 7. Über *Palissya, Stachyotaxus* und *Palaeotaxus*. Handl. K. Sv. Vet.-Akad., 43(8):1–20.

1909. Paläobotanische Mitteilungen. 8. Über *Williamsonia, Wielandiella, Cycadocephalus* und *Weltrichia*. Handl. K. Sv. Vet.-Akad., 45(4):1–38.

1911. Paläobotanische Mitteilungen. 9. Neue Beiträge zur Kenntnis der *Williamsonia*-Blüten. Handl. K. Sv. Vet.-Akad., 46(4):1–33.

1912. Die Mikrosporophylle von *Williamsonia*. Ark. Bot. K. Sv. Vet.-Akad., 12(6):1–10.

NEGER, F. W., E. MÜNCH, and B. HUBER

1952. Die Nadelhölzer (Koniferen) und übrigen Gymnospermen. Sammlung Göschen 355, 140 pp. Berlin: Walter de Gruyter and Co.

NĚMEJC, F.

1950. The natural systematics of plants in the light of the present palaeontological documents. Sborn. Narodn. Mus. Praze (Acta Mus. Natl. Prag.), 6 B(3):1–83.

NOZERAN, R.

1949a. Les inflorescences de *Cephalotaxus*. Comparaison avec des cônes androgynes de Pinacées. Ann. Univ. Montpellier et du Languedoc Méditerr.-Roussillon, Suppl. Sci. Rec. Trav. Inst. Bot., no. 4, pp. 58–64.

1949b. Les rameaux courts reproducteurs de *Ginkgo biloba*. Ann. Univ. Montpellier et du Languedoc Méditerr.-Roussillon, Suppl. Sci. Rec. Trav. Inst. Bot., no. 4, pp. 68–75.

OGURA, Y.

1930–1932. On the structure and affinities of some Cretaceous plants from Hokkaido. I-II. Journ. Fac. Sci. Imp. Univ. Tokyo (sec. 3, Bot.), 2:381–412, 455–483.

OLIVER, F. W.

1902. On some points of apparent resemblance in certain fossil and recent gymnospermous seeds. New Phytol., 1:145–154.

1903. The ovules of the older gymnosperms. Ann. Bot., 17:451–476.

1904. On the structure and affinities of *Stephanospermum* Brongn., a genus of fossil gymnosperm seeds. Trans. Linn. Soc. London, ser. 2, 6:361–400.

OLIVER, F. W., and D. H. SCOTT

1904. On the structure of the Palaeozoic seed *Lagenostoma Lomaxi*, with a statement of the evidence upon which it is referred to *Lyginodendron*. Philos. Trans. Roy. Soc. London., B 197:193–247.

ORR, M. Y.

1937. On the value for diagnostic purposes of certain of the anatomical features of conifer leaves. Notes Roy. Bot. Gard. Edinburgh, no. 94, pp. 255–266.

PEARSON, H. H. W.

1929. Gnetales. vii + 194 pp. Cambridge. Cambridge Univ. Press.

PEIRCE, A. S.

1936. Anatomical interrelationships of the Taxodiaceae. Trop. Woods, no. 46, pp. 1–14.

1937. Systematic anatomy of the woods of the Cupressaceae. Trop. Woods, no. 49, pp. 5–21.

PENHALLOW, D. P.

1896. The generic characters of the North American Taxaceae and Coniferae. Proc. and Trans. Roy. Soc. Canada, ser. 2, 2(sec. 4):33–57.

PENHALLOW, D. P. (Cont.)

1907. A Manual of the North American Gymnosperms. viii + 375 pp. Boston, Mass.: Ginn and Co.

PENNY, J. S.

1947. Studies on the conifers of the Magothy flora. Amer. Journ. Bot., 34:281–296.

PENZIG, O.

1894. Pflanzen-Teratologie. II. 594 pp. Genua: Angelo Ciminago.

1922. Pflanzen-Teratologie, systematisch geordnet. 2nd ed. Vol. 3, 624 pp. Berlin: Gebr. Borntraeger.

PHILLIPS, E. W. J.

1941. The identification of coniferous woods by their microscopic structure. Journ. Linn. Soc. London Bot., 52:259–320.

PILGER, R.

1926. Gymnospermae. *In* A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien. 2nd ed., 13:44–82, 98–109, 121–166, 199–403. Leipzig: W. Engelmann.

1929. Die Sporangiophor-Theorie und die Herkunft der Coniferen. Beih. Repert. Sp. Nov., 56:93–101.

PLANTEFOL, L.

1948. La théorie des hélices foliaires multiples. Ann. Sci. Nat. Bot., sér. 11, 7:155–229; 8:1–154.

POHL, F.

1928. Der einfaltige Pollen, seine Verbreitung und phylogenetische Bedeutung. Beih. Bot., Centr., 45(1):59–73.

POOL, D. J. W.

1929. On the anatomy of Araucarian wood. Rec. Trav. Bot. Néerl., 25:484–620.

POPHAM, R. A.

1951. Principal types of vegetative shoot apex organization in vascular plants. Ohio Journ. Sci., 51:249–270.

PORSCH, O.

1905. Der Spaltöffnungsapparat im Lichte der Phylogenie. xvi + 196 pp. Jena: G. Fischer.

POSTHUMUS, O.

1924. On some principles of stelar morphology. Rec. Trav. Bot. Néerl., 21:111–296.

POTONIÉ, H.

1897–1899. Lehrbuch der Pflanzenpalaeontologie. viii + 402 pp. Berlin: Ferd. Dümmler.

1912. Grundlinien der Pflanzen-Morphologie im Lichte der Palaeontologie. v + 259 pp. Jena: G. Fischer.

POTONIÉ, H., and W. GOTHAM

1921. Lehrbuch der Paläobotanik. vii + 537 pp. Berlin: Gebr. Borntraeger.

POTONIÉ, R.

1952. Zur Morphologie und morphologischen Nomenklatur der Sporites H. Potonié 1893. Paläontol. Zeitschr., 25:143–154.

PROPACH-GIESELER, C.

1936. Zur Morphologie und Entwicklungsgeschichte der weiblichen Blütenzapfen der Cupressaceen. Bibl. Bot., 114(2):1–56.

PULLE, A.

1937. Remarks on the system of the spermatophytes. Pp. 1–17. Utrecht: N. V. A. Oosthoek's Uitgevers-Maatschappij.

1938. The classification of the spermatophytes. Chron. Bot., 4:109–113.

1950. Compendium van de terminologie, nomenclatuur en systematiek der zaadplanten. 2nd ed., 370 pp. Utrecht: A. Oosthoek's Uitgevers-Maatschappij.

QUISUMBING, E.

1925. Stony layer in seeds of gymnosperms. Bot. Gaz., 79:121–195.

RADAIS, M.

1894. Contribution à l'étude de l'anatomie comparée du fruit des Conifères. Ann. Sci. Nat. Bot., sér. 7, 19:165–368.

RAO, A. R.

1943. The structure and affinities of *Taeniopteris spathulata* McCl. Proc. Natl. Acad. Sci. India, 13:333–355.

READ, C. B.

1936–1937. The flora of the New Albany Shale. I. *Diichna kentuckiensis*, a new representative of the Calamopityeae. II. The Calamopityeae and their relationships. Prof. Pap. U. S. Geol. Surv., 185-H:149–161; 186-E:81–104.

1946. A Pennsylvanian florule from the Forkston coal in the Dutch Mountain outlier, northeastern Pennsylvania. Prof. Pap. U. S. Geol. Surv., 210-B:17–28.

RECORD, S. J.

1934. Identification of the Timbers of Temperate North America. ix + 196 pp. New York: John Wiley and Sons.

REED, F., and M. T. SANDOE

1951. *Cordaites affinis:* a new species of Cordaitean leaf from American coal fields. Bull. Torrey Club, 78:449–457.

REHFOUS, L.

1917. Étude sur les stomates. (Thèse.) Univ. Genève, 110 pp. Genève: Jent.

RENAULT, B.

1879. Structure comparée de quelques tiges de la flore carbonifère. Nouv. Archiv. Mus. Hist. Nat. Paris, sér. 2, 2:213–348.

1883. Cours de botanique fossile. III. 241 pp. Paris: G. Masson.

1896. Études des Gîtes Minéraux de la France: Bassin houiller et permien d'Autumn et d'Epinac. IV. Flore fossile. Vol. 2, 578 pp. Paris: Imprimerie Nationale.

REYNOLDS, L. G.

1924. Female gametophyte of Microcycas. Bot. Gaz., 77:391–403.

ROMARIZ, C.

1946. Estudo e revisão das formas portuguesas de *Frenelopsis*. Bol. Mus. Mineral. e Geol. Univ. Lisboa, no. 14, pp. 1–18.

ROTHMALER, W.

1951. Die Abteilungen und Klassen der Pflanzen. Repert. Nov. Spec., 54:256–266.

1951–1952. Die Gymnospermen und der Ursprung der Angiospermen. Wiss Zeit. Martin-Luther Univ. Halle-Wittenberg, 1(4):1–12.

RUDOLPH, K.

1921. Die Entwicklung der Stammbildung bei den fossilen Pflanzen. Lotos, 69:15–34.

RÜHLE VON LILIENSTERN, H.

1928. "Dioonites pennaeformis Schenk," eine fertile Cycadee aus der Lettenkohle. Palaeontol. Zeitschr., 10:91–107.

SACHS, J.

1868, 1874. Lehrbuch der Botanik. 1st ed., xii + 632 pp., 4th ed., xvi + 928 pp. Leipzig: W. Engelmann.

SAHNI, B.

1920. On the structure and affinities of *Acmopyle Pancheri*, Pilger. Trans. Roy. Soc. London, B 210:253–310.

1932. A petrified *Williamsonia* (*W. Sewardiana*, sp. nov.) from the Rajmahal Hills, India. Mem. Geol. Surv. India, Palaeont. Indica, n.s., 20(3):1–19.

1948. The Pentoxyleae: a new group of Jurassic gymnosperms from the Rajmahal Hills of India. Bot. Gaz., 110:47–80.

SAHNI, B., and T. C. N. SINGH

1931. Notes on the vegetative anatomy and female cones of *Fitzroya patagonica* Hook. fil. Journ. Indian Bot. Soc., 10:1–20.

SAKISAKA, M.

1929. On the seed-bearing leaves of *Ginkgo*. Jap. Journ. Bot., 4:219–235.

SANIO, C.

1863. Vergleichende Untersuchungen über die Zusammensetzung des Holzkörpers. Bot. Zeit., 21:356–363, 369–375, 377–385, 389–399, 401–412.

1873–1874. Anatomie der gemeinen Kiefer (*Pinus silvestris* L.). II. Jahr. Wiss. Bot., 9:50–126.

SATAKE, Y.

1934. On the systematic importance of the vascular course in the cone scales of the Japanese Taxodiaceae. Bot. Mag. Tokyo, 48:186–205.

SAX, K., and J. M. BEAL

1934. Chromosomes of the Cycadales. Journ. Arnold Arbor., 15:255–258.

SAX, K., and H. J. SAX

1933. Chromosome number and morphology in the conifers. Journ. Arnold Arbor., 14:356, 375.

SAXTON, W. T.

1934. Notes on conifers. VIII. The morphology of *Austrotaxus spicata* Compton. Ann. Bot., 48:411–427.

SCHAFFNER, J. H.

1934. Phylogenetic taxonomy of plants. Quart. Rev. Biol., 9:129–160.

SCHENK, A.

1867. Die fossile Flora der Grenzschichten des Keupers und Lias Frankens. xxiv + 232 pp. Wiesbaden: Kreidel.

1889. Ueber *Medullosa* Cotta und *Tubicaulis* Cotta. Abh. K. Sächs. Ges. Wiss., math.-phys. Kl., 15:521–558.

SCHLEIDEN, M. J.

1842–1843. Grundzüge der wissenschaftlichen Botanik nebst einer methodologischen Einleitung als Anleitung zum Studium der Pflanze. I–II. Vol. I, xxvi + 289 pp.; Vol. II, xviii + 564 pp. Leipzig: W. Engelmann.

SCHLÜTER, H., and H. SCHMIDT

1927. *Voltzia*, *Yuccites* und andere neue Funde aus dem südhannoverschen Buntsandstein. Neues Jahr. Mineral. Geol. u. Paläontol., B 57:12–27.

SCHMID, W.

1937. Beitrag zur Kenntnis von *Callitropsis araucarioides* Compton. Ber. Schweiz. Bot. Ges., 47:124–159.

SCHMIDT, A.

1924. Histologische Studien an phanerogamen Vegetationspunkten. Bot. Archiv, 8:345–404.

SCHNARF, K.

1933. Embryologie der Gymnospermen. *In* K. Linsbauer, Handbuch der Pflanzenanatomie, div. 2(2), Vol. 10(2). viii + 304 pp. Berlin: Gebr. Borntraeger.

1937. Anatomie der Gymnospermen-Samen. *In* K. Linsbauer, Handbuch der Pflanzenanatomie, div. 2, Vol. 10(1). pp. 1–156. Berlin: Gebr. Borntraeger.

1941. Vergleichende Cytologie des Geschlechtsapparates der Kormophyten. vii + 249 pp. Berlin-Zehlendorf: Gebr. Borntraeger.

1942. Archegon und Archegontheorie. Kritischer Versuch einer Geschichte des Pflanzenarchegons. Biologia Gen., 16:198–228.

SCHOPF, J. M.

1939. *Medullosa distelica*, a new species of the anglica group of Medullosa. Amer. Journ. Bot., 26:196–207.

1948. Pteridosperm male fructifications: American species of *Dolerotheca*, with notes regarding certain allied forms. Journ. Paleontol., 22:681–724.

SCHOPF, J. M., L. R. WILSON, and R. BENTALL

1944. An annotated synopsis of Palaeozoic fossil spores and the definition of generic groups. Rept. Investigations, Ill. Geol. Surv., no. 91, pp. 1–66.

SCHOUTE, J. C.

1903. Die Stelär-Theorie. 175 pp. Jena: G. Fischer.

1925. La nature morphologique du bourgeon féminin des *Cordaites*. Rec. Trav. Bot. Néerl., 22:113–127.

SCHÜEPP, O.

1926. Meristeme. *In* K. Linsbauer, Handbuch der Pflanzenanatomie, div. 1(2), Vol. 4. viii + 114 pp. Berlin: Gebr. Borntraeger.

SCHUSTER, J.

1931. Über das Verhältnis der systematischen Gliederung, der geographischen Verbreitung und der paläontologischen Entwicklung der Cycadeen. Bot. Jahr., 44:165–260.

1932. Cycadaceae. *In* A. Engler, Das Pflanzenreich, 4(1):1–168. Leipzig: W. Engelmann.

SCHWENDENER, S.

1878. Mechanische Theorie der Blattstellungen. iv + 141 pp. Leipzig: W. Engelmann.

SCOTT, D. H.

1897. The anatomical characters presented by the peduncle of Cycadaceae. Ann. Bot., 11:399–419.

1899. On the structure and affinities of fossil plants from the Palaeozoic rocks. III. On *Medullosa anglica*, a new representative of the Cycadofilices. Trans. Roy. Soc. London, B 191:81–126.

1900. Studies in Fossil Botany. xiii + 533 pp. London: A. and C. Black.

1902. The old wood and the new. New Phytol., 1:25–30.

1923. Studies in Fossil Botany. II. (3rd ed.) xvi + 446 pp. London: A. and C. Black.

SELLING, O. H.

1944. On "cupressoid" root remains of Mesozoic age from the Arctic. Ark. Bot. K. Sv. Vet.-Akad., 31 A(13):1–20.

1951. On "Protojuniperoxylon" arcticum. Journ. Paleontol., 25:538–539.

SEWARD, A. C.

1912. A petrified *Williamsonia* from Scotland. Philos. Trans. Roy. Soc. London, B 203:101–126.

1917, 1919. Fossil Plants. Vol. 3, xviii + 656 pp., Vol. 4, xvi + 543 pp. Cambridge: Cambridge Univ. Press.

SHARP, L. W.

1943. Fundamentals of Cytology. x + 270 pp. New York and London: McGraw-Hill.

SIFTON, H. B.

1920. Some characters in xylem tissue in Cycads. Bot. Gaz., 70:425–435.

1922. The bars of Sanio and primordial pit in the gymnosperms. Trans. Roy. Soc. Canada, ser. 3 (sec. 5), 16:83–99.

1944. Developmental morphology of vascular plants. New Phytol., 43:87–129.

SINNOTT, E. W.

1913. The morphology of the reproductive structures in the Podocarpineae. Ann. Bot., 27:39–82.

SKOTTSBERG, C.

1940. Oversikt av växtriket. *In* "Växternas liv," C. Skottsberg, ed., Vol. 5, xviii + pp. 137–735. Stockholm: Nordisk Familjeboks Förlagsaktiebolag.

SLYPER, E. J.

1933. Bestimmungstabelle für rezente und fossile Coniferenhölzer nach mikroskopischen Merkmalen. Rec. Trav. Bot. Néerl., 30:482–513.

SOKOLOWA, C.

1891. Naissance de l'endosperme dans le sac embryonnaire de quelques gymnospermes. Bull. Soc. des Nat. Moscou, n.s., 4:446–497.

SOLMS-LAUBACH, H.

1890a. Die Sprossfolge der Stangeria und der übrigen Cycadeen. Bot. Zeit., 48:177–187, 193–199, 209–215, 225–230.

1890b. Ueber die Fructification von *Bennettites Gibsonianus* Carr. Bot. Zeit., 48:789–798, 805–816, 821–833, 843–847.

1908. Die Bedeutung der Palaeophytologie für die systematische Botanik. Mitt. Philomat. Ges. Elsass-Lothringen, 3:353–362.

SPRECHER, A.

1907. Le *Ginkgo biloba* L. (Thèse.) Univ. Genève, 207 pp. Genève: Atar, S. A.

SRIVASTAVA, B. P.

1946. Silicified plant-remains from the Rajmahal series of India. Proc. Natl. Acad. Sci. India, 15:185–211.

STEBBINS, G. L. Jr.

1948. The chromosomes and relationships of *Metasequoia* and *Sequoia*. Science, 108: 95–98.

1950. Variation and Evolution in Plants. xx + 643 pp. New York: Columbia Univ. Press.

STEFANOFF, B.

1936. Über das Wesen und die Morphogenie des fruchtbildenden Organs bei den Samenpflanzen. Annuaire, Univ. Sophia, sér. 5(2), 14:38–66.

STENZEL, K. G.

1876. Beobachtungen an durchwachsenen Fichtenzapfen. Ein Beitrag zur Morphologie der Nadelhölzer. Nova Acta Leop. Carol., 38:291–334.

STERLING, C.

1945. Growth and vascular development in the shoot apex of *Sequoia sempervirens* (Lamb.) Endl. I. Structure and growth of the shoot apex. Amer. Journ. Bot., 32:118–126.

1947. Sclereid formation in the shoot of *Pseudotsuga taxifolia*. Amer. Journ. Bot., 34:45–52.

1949. Some features in the morphology of *Metasequoia*. Amer. Journ. Bot., 36:461–471.

STEWART, W. N.

1951. *Medullosa pandurata* sp. nov. from the McLeansboro group of Illinois. Amer. Journ. Bot., 38:709–717.

STEWART, W. N., and T. DELEVORYAS

1952. Bases for determining relationships among the Medullosaceae. Amer. Journn. Bot., 39:505–516.

STOPES, M. C.

1904. Beiträge zur Kenntniss der Fortpflanzungsorgane der Cycadeen. Flora, 93: 435–482.

STOPES, M. C., and K. FUJII

1910. Studies on the structures and affinities of Cretaceous plants. Philos. Trans. Roy. Soc. London, B 201:1–90.

STRASBURGER, E.

1872. Die Coniferen und Gnetaceen. ix + 442 pp. Jena: H. Dabis.

1875. Ueber Zellbildung und Zelltheilung. xi + 256 pp. Jena: H. Babis.

1878. Ueber Befruchtung und Zelltheilung. 108 pp. Jena: H. Dabis.

1879a. Die Angiospermen und die Gymnospermen. viii + 173 pp. Jena: G. Fischer.

1879b. Neue Beobachtungen über Zellbildung und Zelltheilung. Bot. Zeit., 37:265–279, 281–288.

1884. Neue Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen als Grundlage für eine Theorie der Zeugung. xi + 176 pp. Jena: G. Fischer.

1891. Ueber den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen. *In* Histologische Beiträge. Vol. 3, xxxii + 991 pp. Jena: G. Fischer.

1892. Über das Verhalten des Pollens und die Befruchtungsvorgänge bei den Gymnospermen. *In* Histologische Beiträge. Vol. 4, x + 46 pp. Jena: G. Fischer.

1894. The periodic reduction of the number of chromosomes in the life-history of living organisms. Ann. Bot., 8:281–316.

STUDT, W.

1926. Die heutige und frühere Verbreitung der Koniferen und die Geschichte ihrer Arealgestaltung. Mitt. Inst. allgem. Bot. Hamburg, 6:167–307.

STUR, D.

1884. Zur Morphologie und Systematik der Culm- und Carbon-Farne. Sitzungsber. K. Akad. Wiss. Wein, math.-naturw. Kl., 88:633–846.

SUGIHARA, Y.

1947. The chromosome numbers in gymnosperms. Jap. Journ. Genet. Suppl., 1:132–138.

SYKES, M. G.

1910a. The anatomy of *Welwitschia mirabilis* Hook. f., in the seedling and adult states. Trans. Linn. Soc. London, ser. 2, 7:327–354.

Sykes, M. G. (Cont.)

1910b. The anatomy and morphology of the leaves and inflorescences of *Welwitschia mirabilis*. Philos. Trans. Roy. Soc. London, B 201:179–226.

Szafer, W.

1949. Studies on the genus *Tsuga* Carr. in the Tertiary of Europe. Bull. Acad. Polon. Sci. et Lettr., Cl. sci. math. et natur., sér. B, I:23–51.

Takhtajan, A. L.

1950. Phylogenetic principles of the system of higher plants. Bot. Journ. Akad. Nauk SSSR, 35:113–139. (See Bot. Rev. [1953], 19:1–45.)

Tammes, P. M. L.

1930. On the Origin of Number and Arrangement of the Places of Exit on the Surface of Pollen-Grains. Proefschrift, Univ. Groningen. 84 pp. Amsterdam: J. H. de Bussy.

Tansley, A. G.

1908. Lectures on the evolution of the Filicinean vascular system. X. A comparison of the vascular system of the ferns with that of other phyla of vascular plants. New Phytol., 7:29–40.

Thibout, E.

1896. Recherches sur l'appareil mâle des gymnospermes. (Thèse.) Fac. Sci. Univ. Lille. 265 pp. Lille: L. Daniel.

Thiergart, F.

1949. Die Sciadopityszone und der Sciadopitys-Vorstoss in der niederrheinischen Braunkohle. Braunkohle, Wärme und Energie, pp. 153–156.

Thoday, M. G., and E. M. Berridge

1912. The anatomy and morphology of the inflorescences and flowers of *Ephedra*. Ann. Bot., 26:953–985.

Thomas, H. H.

1915. On *Williamsoniella*, a new type of Bennettitalean flower. Philos. Trans. Roy. Soc. London, B 207:113–148.

1925. The Caytoniales, a new group of angiospermous plants from the Jurassic rocks of Yorkshire. Philos. Trans. Roy. Soc. London, B 213:299–363.

1930. Further observations on the cuticle structure of Mesozoic Cycadean fronds. Journ. Linn. Soc. London, Bot., 48:389–415.

1933. On some pteridospermous plants from the Mesozoic rocks of South Africa. Philos. Trans. Roy. Soc. London, B 222:193–265.

1938. Pteridosperm evolution and the Angiospermae. Compt. Rend. 2ème Congr. Stratigr. Carbon. (Heerlen, 1935), pp. 1311–1321.

Thomas, H. H., and N. Bancroft

1913. On the cuticles of some recent and fossil Cycadean fronds. Trans. Linn. Soc. London, ser. 2, 8:155–204.

Thompson, W. P.

1910. The origin of ray tracheids in the Coniferae. Bot. Gaz., 50:101–116.

1912. The anatomy and relationships of the Gnetales. I. The genus *Ephedra*. Ann. Bot., 26:1077–1104.

1918. Independent evolution of vessels in Gnetales and angiosperms. Bot. Gaz., 65:83–90.

THOMSON, R. B.

1905. The megaspore-membrane of the gymnosperms. Studies, Univ. Toronto, Biol. ser., 4:1–64.

1909. The megasporophyll of *Saxegothaea* and *Microcachrys*. Bot. Gaz., 47:345–354.

1913. On the comparative anatomy and affinities of the Araucarineae. Philos. Trans. Roy. Soc. London, B 204:1–50.

1914. The spur shoot of the pines. Bot. Gaz., 17:362–385.

1927. Evolution of the seed habit in plants. Trans. Roy. Soc. Canada, ser. 3, 21: 229–272.

1940. The structure of the cone in the Coniferae. Bot. Rev., 6:73–84.

1945. "Polyembryony," sexual and asexual embryo initiation and food supply. Trans. Roy. Soc. Canada, ser. 3, 36(sec. 5):143–169.

THOMSON, R. B., and H. B. SIFTON

1925. Resin canals in the Canadian Spruce [*Picea canadensis* (Mill.) B.S.P.]. An anatomical study, especially in relation to traumatic effects and their bearing in phylogeny. Philos. Trans. Roy. Soc. London, B 214:63–111.

TIEGHEM, P. VAN

1869. Anatomie comparée de la fleur femelle et du fruit des Cycadées, des Conifères et des Gnetacées. Ann. Sci. Nat. Bot., sér. 5, 10:269–304.

1870. Recherches sur la symétrie de structure des plantes vasculaires. Ann. Soc. Nat. Bot., sér. 5, 13:5–314.

1872. Mémoire sur les canaux sécréteurs des plantes. Ann. Sci. Nat. Bot., sér. 5, 16:96–201.

1891a. Traité de botanique. 2nd ed., xxxi + 1855 pp. Paris: Savy.

1891b. Sur les tubes criblés extralibériens et les vaisseaux extraligneux. Journ. Bot. Paris, 5:117–128.

1898. Éléments de botanique. 3rd ed. 1179 pp. Paris: Masson.

TIEGHEM, P. VAN, and J. COSTANTIN

1918. Éléments de botanique. I–II. 5th ed. Vol. I, xv + 619 pp.; Vol. II, xx + 743 pp. Paris: Masson et cie.

TIEGHEM, P. VAN, and H. DOULIOT

1886. Sur la polystélie. Ann. Sci. Nat. Bot., sér. 7, 3:275–322.

1888. Recherches comparatives sur l'origine des membres endogènes dans les plantes vasculaires. Ann. Sci. Nat. Bot., sér. 7, 8:1–660.

TIPPO, O.

1942. A modern classification of the plant kingdom. Chron. Bot., 7:203–206.

TRAVERSE, A.

1950. The primary vascular body of *Mesoxylon Thompsonii*, a new American Cordaitalean. Amer. Journ. Bot., 37:318–325.

UENO, J.

1951. Morphology of pollen of *Metasequoia*, *Sciadopitys* and *Taiwania*. Journ. Inst. Polytech. Osaka Univ., 2(D):22–26.

UNGER, F.

1852. Versuch einer Geschichte der Pflanzenwelt. xvi + 364 pp. Wien: W. Braumüller.

WALTON, J.

1928. On the structure of a Palaeozoic cone-scale and the evidence it furnishes of the primitive nature of the double cone-scale in the Conifers. Proc. Manchester Lit. and Philos. Soc., 73:1–6.

WALTON, J. (Cont.)

1931. Contributions to the knowledge of Lower Carboniferous plants. III. Philos. Trans. Roy. Soc. London, B 219:347–379.

1949a. A petrified example of *Alcicornopteris* (*A. Hallei* sp. nov.) from the Lower Carboniferous of Dumbartonshire. Ann. Bot., London, n.s., 13:445–452.

1949b. *Calathospermum scoticum*, an ovuliferous fructification of Lower Carboniferous age from Dumbartonshire. Trans. Roy. Soc. Edinburgh, 61(3):719–728.

1952. L'évolution des téguments et de la protection du sporange. Ann. Biol. Paris, 28:C 129–132.

WARMING, E.

1873. Untersuchungen über Pollen bildende Phyllome und Kaulome. Bot. Abh., J. Hanstein, ed., 2(2):1–90.

1877. Undersögelser og betranktninger over Cycadeerne. Forhandl. K. Danske Videnskabernes Selsk., pp. 88–144.

WEBBER, H. J.

1901. Spermatogenesis and fecundation of Zamia. Bull. U. S. Dept. Agri., Bur. Plant Industry, 2:1–92.

WEBER, O., and J. T. STERZEL

1896. Beiträge zur Kenntnis der Medulloseae. Ber. Naturwiss. Ges. Chemnitz, 13: 44–143.

WETMORE, R. H.

1943. Leaf-stem relationships in the vascular plants, Torreya, 43:16–28.

WETTSTEIN, R.

1911–1935. Handbuch der systematischen Botanik. 2nd ed. (1911), viii + 915 pp.; 3rd ed. (1924), viii + 1018 pp.; 4th ed. (1935), x + 1149 pp. Leipzig u. Wien: Franz Deuticke.

1925. Die Bedeutung der sero-diagnostischen Methode für die phylogenetisch-systematische Forschung. Zeitschr. indukt. Abstammungs- und Vererbungslehre, 36:438–445.

WHITE, D.

1904. The seeds of Aneimites. Smithson. Misc. Colls., 47:322–331.

WIELAND, G. R.

1899–1901. A study of some American fossil cycads. Amer. Journ. Sci., ser. 4, 7:219–226; 11:423–436.

1906, 1916. American fossil cycads. I–II. Publ. Carnegie Inst. Washington. Vol. 34(1), viii + 296 pp.; Vol. 34(2), vii + 277 pp.

1919. Classification of the Cycadophyta. Amer. Journ. Sci., ser. 4, 47:391–406.

1934. Fossil cycads, with special reference to *Raumeria Reichenbachiana* Goeppert sp. nov. of the Zwinger of Dresden. Palaeontographica, B 79:85–130.

1935. The Cerro Cuadrado petrified forest. Publ. Carnegie Inst. Washington, 449: i–ix, 1–180.

WILDE, M. H.

1944. A new interpretation of coniferous cones. I. Podocarpaceae (*Podocarpus*). Ann. Bot., n.s., 8:1–41.

WILDE, M. H., and A. J. EAMES

1948–1952. The ovule and "seed" of *Araucaria Bidwillii* with discussion of the taxonomy of the genus. I. Morphology. II. Taxonomy. Ann. Bot., n.s., 12:311–326; 16:27–47.

Williamson, W. C.

1851. On the structure and affinities of the plants known as Sternbergiae. Mem. Manchester Lit. and Philos. Soc., ser. 2, 9:340–358.

1871–1893. On the organization of the fossil plants of the coal-measures. I–XIX. Philos. Trans. Roy. Soc. London, vols. 161–184.

Williamson, W. C., and D. H. Scott

1896. Further observations on the organization of the fossil plants of the coal-measures. III. Lyginodendron and Heterangium. Philos. Trans. Roy. Soc. London, B 186:703–779.

Willkomm, M.

1880. Zur Morphologie der samentragenden Schuppe des Abietineezapfens. Nova Acta Leopol.-Carol., 41:331–344.

Wodehouse, R. P.

1935. Pollen Grains; Their Structure, Identification and Significance in Science and Medicine. xiii + 574 pp. New York and London: McGraw-Hill.

Worsdell, W. C.

1897. On "transfusion tissue": its origin and function in the leaves of gymnospermous plants. Trans. Linn. Soc. London, ser. 2 (Bot.), 5:301–319.

1898a. The comparative anatomy of certain genera of the Cycadaceae. Journ. Linn. Soc. London, Bot., 33:437–457.

1898b. The vascular structure of the sporophylls of the Cycadaceae. Ann. Bot., 12: 203–241.

1899. Observations on the vascular system of the female "flowers" of Coniferae. Ann. Bot., 13:527–548.

1900a. The structure of the female "flower" in Coniferae. An historical study. Ann. Bot., 14:39–82.

1900b. The vascular structure of the ovule of *Cephalotaxus*. Ann. Bot., 14:317–318.

1901. Contributions to the comparative anatomy of the Cycadaceae. Trans. Linn. Soc. London, ser. 2 (Bot.), 6:109–121.

1902a. The evolution of the vascular tissue of plants. Bot. Gaz., 34:216–223.

1902b. The morphology of sporangial integuments. Ann. Bot., 16:596–599.

1906. The structure and origin of the Cycadaceae. Ann. Bot., 20:129–159.

Yarmolenko, A. V.

1933. /The experimental application of the anatomy of the secondary wood in the trunk with the view of clarifying the phylogeny in conifers./ Soviets. Bot., 6:46–63.

Zimmermann, W.

1930. Die Phylogenie der Pflanzen. xi + 452 pp. Jena: G. Fischer.

1932. Paläobotanische und phylogenetische Beiträge. I–V. Palaeobiologica, 5:321–348.

1949. Geschichte der Pflanzen. xi + 111 pp. Stuttgart: G. Thieme.

1952. Main results of the "telome theory." Palaeobotanist, 1:456–470.

BIBLIOGRAPHY II

AIRY-SHAW, H. K.

1950. Post-Darwinian development of taxonomy. Lectures on the development of taxonomy, 1948–1949, Linn. Soc. London and Systematics Assoc. Pp. 60–79.

BOWER, F. O.

1938. Sixty years of Botany in Britain (1875–1935). vii + 112 pp. London: Macmillan and Co.

CONSTANTIN, J.

1934. Aperçu historique des progrès de la botanique depuis cent ans (1834–1934). Ann. Sci. Nat., Bot., ser. 10, 16:vii–cciii.

DAWES, B.

1952. A Hundred Years of Biology. 429 pp. London: Gerald Duckworth.

FOTHERGILL, P. G.

1952. Historical Aspects of Organic Evolution. xiii + 427 pp. London: Hollis and Carter.

GOEBEL, K.

1924. Wilhelm Hofmeister. Arbeit und Leben eines Botanikers des 19. Jahrhunderts. 177 pp. Leipzig: Akadem. Verlagsges.

GOTHAN, W.

1948. Die Paläobotanik in Deutschland in den letzen 100 Jahren. Zeitschr. Deutsch. Geol. Ges., 100:94–105.

GREEN, J. R.

1909. A History of Botany, 1860–1900, Being a Continuation of Sach's "History of Botany, 1530–1860." 543 pp. Oxford: Henry Frowde (Clarendon Press).

1914. A History of Botany in the United Kingdom from the Earliest Times to the End of the 19th Century. xii + 648 pp. London: J. M. Dent and Sons.

HARVEY-GIBSON, R. J.

1919. Outlines of the History of Botany. x + 274 pp. London: A. and C. Black.

HILL, T. G.

1932. The advancement of botany. Rept. British Assoc. Advance. Sci., 100th meeting, sec. K, pp. 196–214.

HUBER, B.

1937. Hundert Jahre Siebröhrenforschung. Protoplasma, 29:132–148.

JESSEN, K. F. W.

1864. Botanik der Gegenwart und Vorzeit in culturhistorischer Entwickelung. xxii + 495 pp. Leipzig: Brockhaus.

KÜSTER, E.

1938. Die Entwicklung der Lehre von der Pflanzenelle. *In* L. Aschoff, E. Küster, and W. J. Schmidt, Hundert Jahre Zellforschung. Protoplasma-Monogr., 17:1–64. Berlin: Gebr. Borntraeger.

MÖBIUS, M.

1937. Geschichte der Botanik von den ersten Anfängen bis zur Gegenwart. vi + 458 pp. Jena: G. Fischer.

OLIVER, F. W.

1913. Makers of British Botany. 332 pp. Cambridge: Cambridge Univ. Press.

Reed, H. S.
1942. A Short History of Plant Sciences. 320 pp. Waltham, Mass.: Chronica Botanica Co.

Sachs, J.
1875. Geschichte der Botanik vom 16. Jahrhundert bis 1860. xii + 612 pp. München: R. Oldenbourg.

Schmucker, T., and G. Linnemann
1951. Geschichte der Anatomie des Holzes. *In* H. Freund, Handbuch der Mikroskopie in der Technik, 5(1):1–78. Frankfurt a. M.: Umschau Verlag.

Strasburger, E.
1907. Die Ontogenie der Zelle seit 1875. Progressus rei botanicae, 1:1–138.

Turrill, W. B.
1942. Taxonomy and phylogeny. Bot. Rev., 8:247–270, 473–532, 655–707.

Ward, L. F.
1885. Sketch of paleobotany. Ann. Rept. U. S. Geol. Surv. (1883–1884), 5:i–xxxvi, 1–469.

Willmott, A. J.
1950. Systematic botany from Linnaeus to Darwin. Lectures on the development of taxonomy, 1948–1949, Linn. Soc. London and Systematics Assoc., pp. 33–45.

Wilson, E. B.
1925. The Cell in Development and Heredity. (3rd ed.), xxxvii + 1232 pp. New York: Macmillan and Co.

THE SYSTEMATICS OF THE ANGIOSPERMS[1]

By LINCOLN CONSTANCE
University of California, Berkeley

Historical Sketch

One hundred years ago the flowering plants were customarily arranged in conformity with the various so-called "Natural Systems" of classification, which had by then almost wholly displaced the artificial "Sexual System" of Linnaeus. The most widely accepted classification was perhaps that of A. P. de Candolle, but it was rivaled by those of A. de Jussieu and Brongniart in France and by that of Endlicher in Austria and Germany. John Lindley, in England, proposed some five systems, or modifications of the same one, between 1830 and 1845, but none was ever widely adopted, although he became one of the most vocal protagonists of natural systems in general.

Natural Systems

These classifications, despite differences in detail, had much in common. They all represented elaborations and extensions of the empirical arrangements on the basis of morphological similarity, developed by the later pre-Linnean herbalists; they were strongly foreshadowed by the work of John Ray and the "Fragmenta" of Linnaeus; and they were dependent upon the original formulation by Bernard and A. L. de Jussieu. Tournefort, Linnaeus, and A. L. de Jussieu had firmly established a working concept of genera, but Linnaeus had merely placed these together in highly arbitrary, numerical classes. The problem was now to achieve a grouping of genera into tenable larger categories on the basis of "affinity." Ray's basic division of plants into flowering versus flowerless, and of the former into monocotyledons and dicotyledons, formed the first skeletal structure for such an objective. Robert Brown's elaboration of the distinction between gymnosperms and angiosperms furnished an additional major dichotomy, but gymnosperms were generally considered to be a subgroup of dicotyledons.

De Candolle, in his *Théorie Élémentaire* of 1813, gave clear expression to the objectives, methods, and difficulties of such arrangement. (Candolle and Sprengel, 1821, pp. 104, 112.)

> The solution of the last-mentioned problem, that, namely, of marking out the connections of families with one another, and of so arranging them with respect to each other as Nature has arranged them, is the object of Method, or the Ideal after which Science is incessantly striving, and to which she has recently approached nearer than she ever did before, without having yet perhaps completely reached it. . . . To the Theory of Natural Classification belong essentially the three following particulars. In the *first* place we

1. The reviewer wishes to express his sincere thanks to his colleague, Dr. Adriance S. Foster, for reading this article in manuscript and for his helpful suggestions.

must be acquainted with the relative importance which belongs to organs, compared with one another; in the *second* place, we must know the circumstances which might lead the observer to mistake the true nature of organs; and, in the *third* place, we must be able to estimate the importance which may be attached to each of the points of view, under which an organ may be considered.

Morphology of reproductive structures—seeds, fruit, flowers—was asserted to furnish a reliable basis for determining affinity, and a warning was issued against employing for this purpose physiological characters vital to the functioning of the plants. Abortion, alteration, and union of organs were emphasized as the three basic causes likely to confuse the observer by concealing basic symmetry and hence true affinity. De Candolle (1844) distinguished dicotyledons and monocotyledons, and then divided the former into choripetalous-hypogynous and perigynous-epigynous, sympetalous, and apetalous (including gymnospermous) lines, respectively. Sympetalous types, notably Compositae, were regarded as the climax of the system. In espousing this arrangement, Hooker said (1873, p. 994):

The Cohorts may thus be fancifully likened to the parti-coloured beads of a necklace, joined by a clasp, the beads touching at similarly coloured points of their surfaces. The position of each bead in the necklace is determined by the predominance of colours common to itself and those nearest to it; whilst the number and proportion of the other colours which each bead presents, indicates its claims to be placed elsewhere in the necklace; in other words, such colours represent the cross affinities which the Cohorts display with others remote from the position they occupy.

Endlicher (1836–1840) proposed a similar arrangement, but regarded the choripetalous Leguminosae as capping his scheme; incidentally, he erred in placing cycads and the parasitic and reduced Balanophoraceae and the genus *Cytinus* among the vascular cryptogams. Brongniart's system (1843) is notable chiefly for the attempt to break up the unisexual and/or apetalous dicotyledons and insert them among choripetalous ones. The arrangement of A. de Jussieu (1850) placed monocotyledons before dicotyledons, and within the latter showed a sequence of sympetalous, choripetalous, and gymnospermous orders. By 1873, J. D. Hooker was able to state his acceptance of the following propositions: (1) that the primary division of the vegetable kingdom is into cryptogamic verus phanerogamic plants; (2) that the primary division of phanerogams is into dicotyledons versus monocotyledons; (3) that the primary division of dicotyledons is into angiosperms versus gymnosperms; and (4) that the perianth must be resorted to for further grouping, both in dicots and monocots. The first appearance of the natural system in America was marked by the publication of an American edition of Lindley's *Introduction* in 1831. Torrey and Gray's *A Flora of North America* (1838–1840), was based on the Candollean system.

The following statement by Lindley (1830, p. xvi) affords us as much information as we can perhaps expect on the contemporary conception of the meaning of affinity.

The principle upon what I understand the Natural System of Botany to be founded is, that the affinities of plants may be determined by a consideration of all the points of resemblance between their various parts, properties, and qualities; and that thence an arrangement may be deduced in which those species will be placed next each other which have the greatest degree of relationship; and that consequently the quality or structure of an imperfectly known plant may be determined by those of another which is well known. Hence arises its superiority over arbitrary or artificial systems, such as that of Linnaeus, in which there is no combination of ideas, but which are mere collections of isolated facts, not having any distinct relation to each other. . . . This is the only intelligible meaning that can be attached to the term Natural System, of which Nature herself, who creates species only, knows nothing. It is absurd to suppose that our genera, orders, classes, and the like, are more than mere contrivances to facilitate the arrangement of our ideas with regard to species. A genus, order, or class is therefore called natural, not because it exists in Nature, but because it comprehends species naturally resembling each other more than they resemble anything else.

The era of natural systems of classification had its culmination in the *Genera Plantarum* of Bentham and Hooker (1862–1883), which did not attempt to be a new general system. As remarked by Green (1914, pp. 504–505), "the chief merits of Bentham and Hooker's great work lie below the surface. It is not until we study the arrangements in the orders and the illuminating treatment of the genera and species that we realize how great it is, and what light it has thrown upon Natural Affinities." The work frankly follows the system of de Candolle, since there appeared to be no better alternative at the time, and this system was widely known.

In addition to their general similarity in the arrangements of groups, all the natural systems agreed in being based upon two fundamental concepts: (1) the efficacy of structural similarity as the true guide to affinity and hence proper arrangement, and (2) the special creation and immutability of species. De Candolle wrote (Candolle and Sprengel, 1821, pp. 95–97):

By Species (*species*), we understand a number of plants, which agree with one another in invariable marks. In this matter everything depends upon the idea of invariableness. . . . This idea proceeds on the supposition, that the species which we know, have existed as long as the earth has had its present form. No doubt there were, in the preceding state of our globe, other species of plants, which have now perished, and the remains of which we still find in impressions in shale, slate-clay and other floetz rocks. Whether the present species, which often resemble these, have arisen from them;—whether the great revolutions on the surface of the earth, which we read in the Book of Nature, contributed to these transitions,—we know not. What we know is, that from as early a time as the human race has left memorials of its existence upon the earth, the separate species of plants have maintained the same properties invariably. To be sure, we frequently speak of the transitions and crossings of species; and it cannot be denied that something of this kind does occur, though without affecting the idea of species which we have proposed. . . . Nature seems to prevent the mutual impregation of related species in more ways than one, although these are not completely understood by us.

In Germany, where the natural systems had made comparatively little headway against the Linnaean, the pendulum swung in about 1840 from exclusive preoccupation with "the old and foolish notion, that the sole or chief business of every botanist is to trifle away time in plant-collecting in wood and meadow and in rummaging in herbaria" (Sachs, 1890, p. 187), to more fundamental but hitherto undeveloped phases of plant science. Sachs credits Schleiden with leading the shift in emphasis to the inductive viewpoint that at once changed botany from the status of a purely descriptive to that of a truly natural science, on the same basis as chemistry or physics. Of more immediate importance to systematics, however, were the revival of anatomical investigation by von Mohl and the elaboration of cell formation by Nägeli, although their researches were directed chiefly to cryptogams. Such studies as these paved the way for Hofmeister's ontogenetic studies, culminating in his brilliant generalizations on alternation of generations. For the first time, the apparently major gap between cryptogamic and phanerogamic plants was effectively bridged by the demonstration of a thread of continuity throughout the plant kingdom, a discovery that rendered untenable the concept of separate creation of the different groups. As remarked by Sachs (1890, p. 202):

When Darwin's theory was given to the world eight years after Hofmeister's investigations, the relations of affinity between the great divisions of the vegetable kingdom were so well established and so patent, that the theory of descent had only to accept what genetic morphology had actually brought to view.

Darwin's promulgation of the theory of descent, with its explosive effect on the ideas of special creation and constancy of species, was the major scientific milestone of the nineteenth century in so far as the field of taxonomy was concerned. Apparent doubts and modifications of the concept of species immutability can be gleaned from numerous authors from the time of Adanson and Linnaeus onward. It was not, however, until the full-fledged emergence of the Darwinian thesis in 1859 that there was any major impact on classification. It should not be overlooked that Joseph Hooker was an active party to the development of the Darwinian theory before it took concrete form, and that he was the chief source of botanical data in support of it. Darwin wrote Hooker in 1845, "I assure you deliberately that I consider all the assistance which you have given me is more than I have received from anyone else, and is beyond valuing in my eyes" (L. Huxley, 1918, p. 492). Hooker's experiences aboard the *Erebus* in the southern hemisphere, like those of Darwin on the *Beagle,* turned his interest to a life-long preoccupation with the geographical distribution of plants, notably the occurrence of arctic species in antarctic lands. The subsequent Himalayan travels and the vast familiarity with plants of all parts of the world, acquired as they poured into Kew, made Hooker less dogmatic than most of his contemporaries in regard to the status of species and genera. He adhered to the tenet of fixity of species as a working hypothesis, however, and remained Darwin's friendly and judicious critic for more than a decade. In 1860 he wrote Harvey: "Remember that I was aware of Darwin's views *fourteen years* before I adopted them, and I have done so *solely* and *entirely* from independent study of plants themselves" (L. Huxley, 1918, pp. 519–520). Much of the excellence of Darwin's finished presentation may well be ascribed to his constant rewriting of his ideas to meet Hooker's penetrating criticisms. Once the theory of descent was fully formulated, however, Hooker, together with Thomas Huxley, became one of its staunchest early converts and defenders. It was not until the following decade that such men as A. de Candolle, Bentham, and Asa Gray became active adherents of the evolutionary conception. Gray wrote A. de Candolle in 1863: "Well, as to origin of species, you have now gone just about as far as I have, in Darwinian direction, and both of us have been led step by step by the facts and probabilities, and have not jumped at conclusions" (Gray, 1893, p. 498). Gray's critical attitude toward some aspects of the theory of natural selection was not based upon doubts as to the mutability and variation of species, but rather on a religious predilection for "design" in Nature and a skepticism as to whether natural selection could accomplish all that its exponents attributed to it.

The Darwinian theory provided the long-sought key to the "affinities" recognized by followers of the natural systems. It was now clear that "affinity" could be explained only in terms of actual genetic relationship, and that any natural classification must be based upon lines of evolutionary development. As a result of this stimulus there began to emerge the ostensibly phylogenetic systems, which hold the field at the present time. Although Hooker was convinced of the truth of evolution by modification, Bentham was not fully converted when work on the *Genera Plantarum* got under way, so no mention was made of the theory in that classic.

Phylogenetic Systems

The change from natural to phylogenetic systems of classification was not a sharp one, but a scarcely perceptible transition in many cases. It is difficult to determine whether certain classifications were intended by their authors to be evolutionary or not, and there are differences of opinion in this respect with regard to the underlying philosophy of even the Englerian "Principles" (Blake, 1935; Lawrence, 1951). This system, like that of Warming's, was based on the arrangement of Eichler (1875); Eichler's, in turn was based on that of Braun, who was opposed to the theory of descent (Baron, 1931). Thus, Turrill (1942, p. 671) says, "Engler's system does not claim to be phylogenetic in the complete sense but to show in its sequence of groups progressive complexity of structure, apart from accepted subordinate reductions." On the contrary, I am inclined to believe (on the basis of my own rough translation of the *Principles of Systematic Arrangement,* Engler, 1936) that Engler *did* intend his system to be phylogenetic, if due allowance is made for his concept of an essentially autonomous origin and evolution for almost every plant family. These begin with the statement (*ibid.,* p. ix):

> The endeavor of the scientific classification of plants, or systematic botany, is directed chiefly toward grouping plant forms according to their natural relationship into assemblages of lower and higher grade. . . . When natural relationship is spoken of here, this is an undoubted redundancy, for relationship in the true sense of the word is always a natural one.

Immediately thereafter follows a criticism of the older systematists for misusing the term "relationship" to cover instances of mere similarity in a given feature, as opposed to "actual genetic relationship" expressed by agreement in ontogeny and anatomy of organs, chemical characteristics, and the possibility of a common origin in the same part of the earth. Engler emphasized the great diversity of unicellular organisms and their manifold developmental tendencies, and suggested that the various stocks of living species were early differentiated from each other genetically and separated from each other geographically. He stressed parallel courses of evolution, and the danger of mistaking analogies, i.e., the attainment of comparable evolutionary stages in different structures, for evidence of genetic affinity. Species were stated to be capable of giving rise to divergent descendants or of mutating, presumably in parallel directions under similar conditions at different places. These ideas are extended to suggest the possible origin and development of completely distinct stocks—the concept of polyphyletic origin of angiosperms.

> The problem of scientific systematics is, however, not merely to unite the forms distinguished by common traits with groups of lower or higher rank, but it must strive

toward the goal that in the arrangement of plants the genetic evolution or at least the morphological sequences express themselves (*ibid*, p. xvi).

He indicated strong skepticism that angiosperms had arisen from any living gymnosperms, that monocotyledons arose from dicotyledons or vice versa, that sympetalous or apetalous families of dicots were derived from existing choripetalous ones, or even that any living or extinct family had arisen from another. Instead, he devoted himself to tracing the "progressions," or evolutionary morphological stages through which he believed the members of different family stocks had advanced. The idea of a "flower" was extended downward to the vascular cryptogams, and a logical sequence of naked, to apetalous, to choripetalous, to sympetalous flowers was indicated as a major evolutionary trend and given great weight in his system of arrangement.

The Englerian system has achieved wide acceptance as a basis for the arrangement of families in manuals and herbaria, both in Germany and in the United States. In England, Rendle (1904, 1925) followed it closely, but it cannot be said to have displaced there the arrangement of Bentham and Hooker. Wettstein (1924) likewise adhered closely to the Englerian sequence and attempted to bring it more closely into conformity with his own ideas of phylogeny. For example, he attempted to trace a logical development of "floral types" from extinct gymnosperms via Gnetalean-like inflorescences to apetalous dicotyledons, to derive monocots from dicots, and to provide a logical explanation of the change from open to closed pollination. The fact that Wettstein's book has not been translated into English has doubtless militated against its having a wider influence than it has enjoyed. The *Stammbaum* offered by Janchen (1932) provides a graphic summary of Wettstein's views on the arrangement of families.

The systems mentioned thus far agree in visualizing the angiosperms as having arisen from some form of gymnospermous plant with unisexual strobili, as having been primitively wind-pollinated, and as having developed a floral envelope of varying complexity from originally naked flowers. There is the further connotation that woody, catkin-bearing dicotyledons have probably had a distinct origin from that of choripetalous or sympetalous groups, and that the angiospermous flower has arisen from gymnospermous inflorescences.

A quite different train of development is postulated for angiosperms by such workers as Bessey, Hallier, and Hutchinson, who developed their respective systems on the foundation of the de Jussieu-de Candolle-Bentham and Hooker natural systems. Bessey (1897, 1915) formulated a scheme of classification of angiosperms which has gained wide acceptance in the United States as a teaching device. The classification assumes that flowering plants have had their origin from "cycadean strobiliferous ancestors" and that the individual flowers of angiosperms have their homologues in Bennettitalean bisexual strobili. The author's general and special ideas of evolutionary sequence were set forth in a series of very explicit dicta. The primitive angiosperm was indicated to have been a woody, unbranched dicotyledon with simple, opposite, evergreen leaves, and entomophilous, polymerous, bisexual flowers with perianth, androecium, and gynoecium composed of an indefinite number of free, spirally arranged parts. This prototype was believed to correspond to a Ranalian flower, and the Ranalian Plexus was therefore regarded as the point of divergence for the monocotyledons (via Alismatales) and for a hypogynous line (Strobiloideae) and a perigynous-epigynous line (Cotyloideae) of dicotyledons, terminating in Labiatae and Compositae, respectively. Apetalous dicots were all referred to predominantly choripetalous orders, and "reduction" was heavily stressed. The three-dimensional depiction of Bessey's system by Rodríguez (1950) is particularly instructive. The actual sequence of groups closely followed that of Bentham and Hooker, and it may be questioned whether the dicta were not drawn from observations on this arrangement, rather than the arrangement of orders determined by application of the dicta. Bessey specifically cautioned (1897, p. 169):

> And let it be fully understood that this is not presented as final, or as entirely satisfactory; it is merely a working hypothesis which claims no other merit than that of an attempt at conformity to the suggestions sometimes faint, sometimes doubtful, from palaeontology, from embryology (ontogeny), and from morphology.

There were recognized in all some 300 families under 32 orders, with the briefest kind of skeletal descriptions. The classification is readily presentable in graphic form and the postulated evolutionary trends may be easily grasped. Among the chief objections to the system are the gross oversimplification which results in ponderous and polymorphous orders, the lack of substantiation for some of the basic evolutionary assumptions, the great weight accorded hypogyny versus perigyny-epigyny, and the scant attention given to tropical groups. More than any system proposed before it, however, the Besseyan served to emphasize the objective of basing classification squarely on presumed phylogeny. Hallier (1905) asserted, similarly, the monophyletic character of the angiosperms, the primitiveness of the Magnolian floral type (which he believed to have been derived directly from cycadophyte ancestors), the origin of monocotyledons from dicotyledons, and the unnatural character of such divisions as Apetalae and Sympetalae. "The Amentiferae" he regarded as the "highest and most reduced types of one of the lines of Dicotyledons" (1905, p. 154). Later, he decided (1912) that Berberidaceae, rather than Magnoliaceae, represented the key primitive group of angiosperms.

Hutchinson, like Bessey and Hallier, stressed the theme that "a phylogenetic system of classification should be the ultimate aim of taxonomy. In fact the description of every new genus, every new species or form of plant, may be regarded as a contribution towards this end" (1926, pp. 1-2). From his extensive experience with African plants, Hutchinson pointed out the difficulty of characterizing large groups by a general tendency founded on a single structure, and believed that a more natural system might be obtained by the recognition of smaller groups bound together by a combination of characters. Thus, his classification admits 332 families in 105 orders. The major peculiarity of this system is the recognition within the dicotyledons of two major parallel lines of development: a woody one stemming from arborescent Magnoliales, and a herbaceous one arising from herbaceous Ranales. In his volume on monocotyledons, Hutchinson (1934) proposed a quite original classification. Although monocots were regarded as a monophyletic offshoot of herbaceous Ranalian dicots, it was suggested that the group was early differentiated into three principal (and a number of minor) evolutionary lines: (1) Calyciferae, with a biseriate perianth and a rhizotomous habit; (2) Corolliferae, with a uniseriate perianth and a bulbose or cormose habit; and (3) Glumiflorae, branching from the latter, with reduced floral structure. Many monocot families were regarded as "climax" orders, in the delimitation of which the nature of the inflorescence was esteemed as more decisive than the position of the ovary. This system counters the defects noted in the Besseyan scheme with regard to oversimplification of the major groups, overemphasis on hypogyny verus perigyny-epigyny, and neglect of tropical families. The stress on the major dichotomy between predominantly herbaceous as against predominantly woody lines, and the resultant characterization of certain orders as polyphyletic, are features which have worked against its more general acceptance. It seems to be agreed, however, that Hutchinson's proposed phylogenetic classification of monocotyledons is by far the best which has been proposed. His interest in geographical distribution (with its implied endorsement of the theory of continental drift), the full description of orders and families, and the abundant illustrations make his volumes among the most useful and stimulating reference books on systematic botany.

In Defense of the Phylogenetic Point of View

Although the theory of evolution completely revolutionized the underlying philosophy of biological classification, it brought with it no new data, as Mason (1950) emphasizes, so that the chief distinction between natural and phylogenetic classifications was the interpretation of morphological characters in terms of assumed evolutionary trends by the latter (Thoday, 1939). The earlier workers were sanguinely optimistic that comparative morphology, alone, would provide a satisfactory basis for a truly phylogenetic arrangement of angiosperms (Hallier, Bessey; Crow, 1926; Schaffner, 1934). Thus Sargant declared that, "the origin of Angiosperms is perhaps the most important problem which botanical morphology has yet to solve" (1908, p. 121). Serological investigation, according to the claim of Mez and Ziegenspeck (1926), put phylogeny on an experimental basis and fully confirmed morphologically established evolutionary sequences.

A strong reaction, however, soon set in, based primarily upon: (1) the visibly major element of speculation embodied in all phylogenetic schemes (Lam, 1936; W. W. Smith, 1936; Sprague, 1940; Turrill, 1942; Danser, 1950; Metcalfe and Chalk, 1950); (2) the failure of the paleobotanical record to reveal the necessary forms connecting discrete modern groups (Arber, 1925; Turrill, 1938; Swamy and Bailey, 1949; Axelrod, 1952); (3) the inability of systematists to agree on what characters or taxonomic groups are to be considered primitive and what advanced or derived, and hence which morphological sequences are validly phyletic (Zimmermann, 1930; Bremekamp, 1931, 1939; Turrill, 1938, 1942); (4) the improbability of major living groups having given rise to one another (J. Hutchinson, 1923–1924, 1929; Engler; Gunderson, 1939b; Sporne, 1948, 1949); (5) the questioning of the principal canons of classical morphology established in the pre-evolutionary period (Zimmermann, 1930; Thomas, 1932; Arber, 1933, 1937; Lam, 1936, 1948a, 1948b, 1950, 1952; Watson, 1943); (6) the apparent conflict between phyletic seriations propounded upon different kinds of evidence (Hayata, 1921, 1931; Turesson, 1930; Gilmour, 1940; J. S. Huxley, 1940; Watson), and (7) the presumed sacrifice of a classification of maximum utility in favor of one acceptable phylogenetically (Sprague, 1925; Turrill, 1936, 1938, 1942; Gilmour; Gilmour and Turrill, 1941; Watson; Tutin, 1952).

Arber, convinced that "the Natural Selection hypothesis is not the master key to the mysteries of the organic world," urged a return to the pre-evolutionary goal of "the comparative examination of form, studied in itself and for its own sake" in pursuit of general laws of symmetry (1925, pp. 1, 10). Bremekamp asserted (1939, pp. 401–402):

We come therefore to the conclusion that the arrangement of the units of a group in an ascending series is impossible: a direct determination of their age is out of the question, because the historical evidence is entirely inadequate, and the methods for an indirect determination are untrustworthy.

A number of English workers, apparently impressed by the incomplete coincidence of genotypic and phenotypic boundaries in some groups and the problems of efficient arrangement of specimens in large herbaria, have argued for a "general classification" based on a maximum correlation of attributes, and relegated phylogeny to the realm of subsidiary special classifications. It is not clear to me why there should be any fundamental discrepancy between such a general system and one expressing evolutionary relationships. (For an interesting discussion of phylogeny and taxonomy, see Gilmour *et al.*, 1940.)

In advocating his "dynamic system," Hayata solved problems of seriation by regarding *all* resemblances between plants as equally significant and due to their possession of the same genes, these genes having always existed and being fated always to continue to exist. Thus, no taxonomic group has any one fixed natural position, but may have as many natural positions as there are criteria for comparison.

Consequently, the ideal system showing all the relations of every two or every group of more than two of all the families, separately as well as jointly, successively as well as simultaneously, is something like a net of infinite extent with innumerable millions of crystal beads, each on a mesh of a different colour, and each reflecting the images of other beads (Hayata, 1921, p. 177).

The genetic mechanisms underlying such an extraordinary scheme are not clear.

Zimmermann, Lam, Danser, and other representatives of the "telome" school, have concluded that evidence of true evolutionary relationship can emerge only from the fossil record. Meanwhile, they devote themselves to the construction —on the basis of morphological "facts"—of typological series for any given structure or organ (*Merkmalsphylogenetik*), wholly independent of all the other characters of the organisms concerned, as a substitute for *Sippenphylogenetik* or group-phylogeny, which Danser characterizes as "a plausible phantasm" (1950, p. 177).

Now the pendulum appears to be swinging back again, but to a position in which we recognize phylogeny as the ideal towards which systematic arrangement is directed, without our being overly hopeful of attaining that goal quickly or by means of any one kind of evidence. No existing classification is regarded as adequately expressing natural relationships (Sprague, 1940; G. H. M. Lawrence, 1951) but, as Gleason aptly comments: "For the past century all revisions of classification have been made in the hope of a better expression of the course of evolution" (1952, p. 16). The new emphasis is on the correlation of evidence from all available fields, in the conviction that this is our best and only guide to true relationship (Copeland, 1940; Sprague, 1940; Sporne; Mason, 1950; Bailey, 1949, 1951; Eames, 1951; Constance, 1951; Rollins, 1952). Swamy and Bailey have cautioned us (1949, pp. 203–204):

> Before attempting to arrange surviving angiosperms in phylogenetic series, it is essential to obtain reliable evidence regarding salient trends of evolutionary specialization in the various organs and internal structures of these plants. Such evidence can be acquired only by comprehensive and time-consuming investigations of the dicotyledons and monocotyledons *as a whole.*

A quarter of a century ago H. M. Hall wrote (1928, pp. 4–5):

> The adoption of phylogeny as the guiding principle in the classification of animals and plants would seem naturally to follow the acceptance of the theory of evolution. . . . But whether classed as a method or merely as an attitude of mind, it is essential that the phylogenetic spirit furnish the background for every system of classification.

This statement would appear to be equally valid today.

Phylogenetic Indications From Systematic Data

In a recent short note, arrestingly titled "Phylogeny of Flowering Plants: Fact or Fiction?", Tutin makes this challenging statement (1952, p. 26):

> In the ninety-two years since the publication of the "Origin of Species" a great deal of argument but remarkably little fact has been produced about the relationships of the Angiosperms. . . . Meanwhile, neither paleobotany, morphology, anatomy or cytology has thrown any light on the origin of the Angiosperms or of any major group within the Angiosperms which an unbiased observer can regard as unequivocal. Indeed, one may go further and say that no more is known now about the origin of any major group of plants than was known in 1859.

The balance of the present paper will be devoted to attempting to find what indications of phylogeny, if any, may be safely drawn from data now available through a century of progress in a few selected botanical disciplines. Attention will be restricted primarily to comparative morphology, anatomy, embryology, and biochemistry. Evidence from cytology and genetics is intentionally omitted because of limitations in space and time, the fact that it has received the bulk of attention in recent years, that it is rarely applicable above the generic level, and that it has already been so ably summarized recently, notably by Stebbins (1950) and Clausen (1951). This reviewer has had an opportunity to express himself in regard to a few aspects of the bearing of these fields upon taxonomy (Constance, 1951, 1953). At the close of the paper, three classical problems of phylogeny and classification will be briefly considered in the light of information drawn from the various fields. These problems are: (1) the primitive habit of angiosperms; (2) the status of "the Amentiferae" and hence of the Englerian sequence; and (3) the origin and relationships of the monocotyledons.

In the preparation of this material, I have attempted to read as much as possible of the pertinent literature of the past few decades, starting with current publications and working backward. In general, I have not attempted to go beyond the twentieth century, in the belief that the morphological classics of the previous century are widely known and generally available. It is hoped that the bringing together of as complete a bibliography as possible on the supposed phylogeny of angiosperms may be of use even though this reviewer's interpretations may not be accepted. I am only too conscious of the fact that many important omissions have been made, but I have been as thorough as time and available resources permitted.

Wood Anatomy

The most firmly established series of unidirectional phylogenetic trends within the angiosperms are undoubtedly those having to do with features of the secondary xylem. Bailey (1949, 1953) has indicated that the possession of tracheary tissue is a significant mark of land plants at least as far back as the Devonian. He emphasizes the dual role of this tracheary tissue in conduction and in affording mechanical support, and shows how efficiency of transport has been obtained through changes of form and loss of protoplasmic contents by tracheary elements, culminating in the development and specialization of vessels, and provision of mechanical strength through the physical structure and chemical constitution of the cell walls.

> The major trends of phylogenetic modification of the tracheary tissue of the Land Plants are associated with changes of equilibrium between these two fundamentally important physiological functions. . . . These salient trends of evolutionary specialization of the tracheary tissues are largely unidirectional and irreversible, and are fully preserved in surviving angiosperms. There fortunately are no serious missing links in these phylogenetic chains and it is not essential, for example, to search geological strata for vesselless proangiosperms since ancestral types of primitive xylem occur in living representatives of both the dicotyledons and the monocotyledons (Bailey, 1949, p. 66).

The classic work of Bailey and Tupper (1918) in measuring tracheary cells from a very broad range of plant groups represents, in the words of Metcalfe and Chalk, "the beginning of a new period of phylogenetic wood anatomy" (1950, 1:xlii). Bailey and Tupper found that the length of cambial cells and their derivatives is progressively reduced in advancing series of vascular plants. Basing his work on this fundamental principle, Frost (1930a, 1930b, 1931) established a sequence of vessel types in angiosperms. He reasoned that, if a vessel segment is derived from a transformed tracheid, then a primitive vessel should have a maximum of tracheid-like characters, viz., great length, small diameter, angular outline, uniformly thin walls, and very slight development of end walls. By statistical methods he was able to show that such vessel types are correlated with exclusively scalariform perforations. Frost then constructed a phylogenetic sequence of types of vessel pitting, beginning with scalariform and culminating with transverse-porous. Kribs (1935) employed this sequence of vessel types as a basis for an attempted development of a phylogenetic sequence of wood rays. He found that, statistically, heterogeneous rays tend to be associated with wood containing scalariform vessel elements and homogeneous rays with porous vessel elements. He was able on this basis to classify all wood rays into six groups of varying grades of evolutionary specialization. The subsequent studies by Barghoorn (1940, 1941a, 1941b), introduced ontogenetic data and some needed cautions against the tendency to oversimplify ray classification. According to Metcalfe, "The investigation of phylogenetic trends on the basis of ray structure is not very satisfactory, however, because the different classes of ray are not very well defined" (1946, p. 168). A correlation of type of lenticel with type of ray was attempted by Wetmore (1926), who regarded transverse lenticels as primitive in comparison with longitudinal ones. Later, Kribs (1937) used the same statistical approach to establish a sequence of the types of distribution of wood parenchyma, ranging from apotracheal, or diffuse and metatracheal, to the more specialized paratracheal or vasicentric types. Gilbert (1940) asserted that the advanced condition of ring-porosity occurs only in the north temperate zone and without any correlation with the ray types defined by Kribs. It seems clear that the form and distribution in the wood of rays and parenchyma should not be used alone in any endeavor to construe stem anatomy phylogenetically.

Chalk found it possible to classify all dicotyledonous woods into three groups of different degrees of specialization on the basis of the occurrence of vessels with scalariform perforations, fiber-tracheids, and storied structure of the wood. The same methods were extended to the woods of fossil dicots, and his observations tended to show "that the characters regarded as unspecialized by the wood anatomist were relatively more common in the past" (1937, p. 423). The close similarity of such woods as the fossil *Homoxylon* to both cycadophytes and vesselless Ranalians has been used as indicating either direct derivation of the angiosperms from, or their close affinity with these gymnosperms (Sahni, 1932, 1935; Wieland, 1933, 1934; Gupta, 1934; Hsü and Bose, 1952).

The basic sequences established by Frost and Kribs have been correlated with a number of other features of wood anatomy, so that a continually growing list of phylogenetically significant wood characters has been made available for purposes of taxonomic comparison. These have been summarized by Vestal (1937, 1940), Tippo (1938, 1946), Moseley (1948), Cox (1948a, 1948b), and Hall (1952). The intensive application of anatomical criteria to different groups of woody dicotyledons either for clarification of external affinities, or for better classification of constitutent groups may be exemplified by the following: Gruinales and Terebinthales (Kribs, 1930; Webber, 1936, 1941; Heimsch, 1940, 1942, Stern, 1952), Guttiferales and Parietales (Tupper, 1934; Vestal, 1937; Taylor, 1939); Juglandales (Heimsch, 1938; Heimsch and Wetmore, 1939; Withner, 1941), Malvales (Chattaway, 1932, 1937; Webber, 1934), Ranales (Garratt, 1933a, 1933b, 1934; McLaughlin, 1933; Bailey and Smith, 1942; Bailey, Nast and Smith, 1943; Bailey, 1944a; Bailey and Nast, 1945a, 1945b, 1948; Lemesle, 1946a, 1946b, 1946c, 1948, 1953; Nast and Bailey, 1946; Bailey and Swamy, 1948, 1949; Swamy and Bailey, 1949, 1950; Swamy, 1949; Money, Bailey and Swamy, 1950), Urticales (Tippo, 1938, 1940), Betulaceae (Hall, 1952), Casuarinaceae (Moseley), Ericaceae (Cox), Icacinaceae (Bailey and Howard, 1941), and Lecythidaceae (Diehl, 1935). Lists of supplementary features suitable for comparative study and identification, but without phylogenetic seriation, have been supplied by Record (1936), Record and Chattaway (1939), Metcalfe (1946), and Metcalfe and Chalk. Metcalfe and Chalk's monumental compendium of anatomical data, like that of Solereder before it, provides information on most dicotyledonous families and a very rich bibliography. It would perhaps not be out of place to remark, however, that such data are as yet extremely fragmentary for the majority of plant families.

There is some evidence to suggest that the development of vessels in primary xylem has paralleled that of those in the secondary xylem (Bailey, 1944b).

Little has as yet been published with regard to the phloem of dicotyledons, but the pioneer work of Hemenway (1913) appears to indicate that the phylogenetic development of the sieve tube may to some extent parallel that of the vessel element. The present status of our "meager and fragmentary" knowledge of evolutionary trends of specialization in the phloem has recently been summarized by Esau, Cheadle, and Gifford (1953). From a study of the monocotyledons it appears that sieve tubes have undergone a progressive localization of sieve areas on the end walls, a gradual shift from oblique to transverse end walls, a change from compound to simple sieve plates, and a progressive decrease in the prominence of sieve areas on the side walls. The sequence of development of sieve tubes in dicots has yet to be established. In an extensive series of investigations on monocots, Cheadle and his co-worker (Cheadle, 1937, 1938, 1939, 1942a, 1942b, 1943a, 1943b, 1944, 1948; Cheadle and Uhl, 1948; Cheadle and Whitford, 1941) have established apparently phylogenetic trends in the form and distribution of vessels and sieve tubes, and in the types of vascular bundles. Most important, perhaps, is the discovery that in monocotyledons vessels develop first in the roots and spread thence to the aerial parts; in contrast, the sieve tubes are believed to have become modified in the aerial parts, and to have progressed basipetally toward the root.

Wood anatomists have been, in the main, extremely modest in making claims as to the evolutionary significance of their data, and as to its utility for the problems of the taxonomist. It has been emphasized repeatedly (Metcalfe, 1944, 1946; Bailey and Howard, 1941; Tippo, 1946; Bailey, 1949, 1951) that apparently close affinity in structure may be due to parallel or convergent evolution rather than to any close genetic relationship, and that anatomical data are more valuable in indicating that a proposed phylogenetic connection is impossible rather than that it is probable (Bailey, 1944b; Swamy and Bailey, 1949). Thus, the anatomical method is to be regarded as an auxiliary one (Fritsch, 1903; Solereder, 1908; Record, 1934; Vestal, 1937, 1940; Cheadle, 1942a; Chalk, 1944; Metcalfe, 1946), but one which has the advantage that its postulated trends of phylogenetic specialization have been propounded quite independently of preconceived ideas as to the primitiveness of any particular group of angiosperm, or of their derivation from any particular type of ancestor (Tippo, 1938, 1946; Vestal, 1940). In the words of Bailey, "If a truly natural classification is to be attained, it must be based upon the analysis and the harmonization of evidence from *all* organs, tissues and parts" (1949, p. 66).

Other Vegetative Characters

The existence of conflicting theories, bolstered by little convincing substantiating evidence, characterizes the analysis of phyletic trends in regard to the vegetative structures of angiosperms. That the stems of primitive flowering plants were unbranched or little branched, and that derived types exhibit richer ramification, has been postulated by Arber and Parkin (1907), Bessey, Bews (1927), and Corner (1949). Nodal and petiolar anatomy were regarded by Sinnott (1914) as being essentially conservative. He suggested that the trilacunar condition might be primitive and both the multilacunar and the unilacunar states derived, as indicated by the persistence of a trilacunar arrangement in seedlings. The basic character of the trilacunar node appears to have been rather generally accepted, as by Hunt (1937), Dormer (1945), and Sporne, but Croizat (1940) and Ozenda (1949) both regard the multilacunar node as the original type. Ozenda believes that the return to a multilacunar condition in such dicot families with sheathing leaf bases as Polygonaceae and Umbelliferae is due to a "surevolution" or reversion to a quasiprimitive state. Sinnott mentioned the plastic and variable condition of the node in woody Ranales and Kumazawa (1930) reported the occurrence of both trilacunar and unilacunar situations within *Ranunculus.* In a resumé of their work with woody Ranalians, Bailey and his associates (Money, Bailey and Swamy, 1950) report that those families with monocolpate (or derived) pollen and ethereal oil cells form two presumably natural alliances of ten families each, the one showing unilacunar, the other tri- or multilacunar nodes. Whitaker (1933) thought that he had found some correlation among these families between the possession of trilacunar nodes and 19 pairs of chromosomes, and unilacunar nodes and 14 chromosome pairs. In a recent review of petiolar anatomy, Hare (1944) concluded that, although the petiole provides a fresh set of supplementary characters for purposes of classification, it should be regarded primarily in terms of mechanical adaptation and as having "little phylogenetic significance" because of the abundant parallelism in unrelated families, a view shared by Dehay (1941) and Metcalfe and Chalk. The wide occurrence of both the unilacunar and the trilacunar node in Ranalian groups suggests that these conditions may be equally primitive.

From the major and diverse uses which have been made of them from the very dawn of plant classification, one may readily agree with Arber that "there seems to be no room for doubt that phyletic indications, external and internal, are carried by the leaves" (1925, p. 8). Attempts to place these evolutionary trends in a generally agreed upon order have been conspicuously less successful. In regard to leaf position, Schellenberg (1928) viewed the distichous arrangement, Salisbury (1926) and Winkler (1936a) the tristichous, as basic; von Veh (1930) believed that all monocotyledons could be derived from a distichous condition, all dicotyledons from a tetrastichous one. Haccius (1939) suggested that all dicot arrangements could be derived from two fundamental types, and that a truly distichous condition can be attained by different routes. An evolutionary sequence from spiral or alternate to decussate or verticillate is visualized by Hallier, Hutchinson, Dormer (1945), and Sporne, and a trend in the reverse direction by Bessey (1915) and Sprague.

Concepts as to the primitive characters of angiosperm leaves lean heavily upon the presumed antecedents of the group. Thus, Arber and Parkin, and Wieland (1929, 1931, 1933) suggested that if leaves of early angiosperms were compound, the existence of the group might have been long disguised in the fossil record by their resemblance to those of seed ferns or cycadophytes. Hallier (1912), reversing his earlier advocacy of simple Magnolian leaves as primitive, read archaic qualities into the pinnately compound foliage of Berberidaceae. Several authors have indicated a belief that palmately or ternately divided, lobed, or at least veined leaves were either primitive in flowering plants (Sinnott, 1914; Coy, 1928; Winkler, 1936a; Gunderson, 1943), or at least intermediate between ancestral compound leaves and more modern, simple ones (Wieland).

On the other hand, apparently drawing a parallel with modern tropical forest types, Bessey, Parkin (1923), and Bews conceived of ancestral angiosperm leaves as being simple, entire, and evergreen. Winkler and Gunderson regarded pinnate division, lobing, or venation as derived from palmate, while Corner believes the palmate derived from the pinnate by shortening of the axis. The fossil record, according to Croizat, indicates that penninerved leaves are fully as primitive as either palmate or lobed ones, and questions "that the evolution of the leaf of existing Angiosperms began with ancestors of a comparatively uniform leaf-pattern" (1940, p. 56), a point emphasized also by Sprague. The relative antiquity of stipules was stressed by Thomas (1932) and Sporne. Within Leguminosae, Dormer (1945, 1946) supports a sequence from highly compound, pulvinate, and stipulate leaves to less compound, estipulate, and epulvinate. Arber considers the leaves of monocotyledons to be "replacement organs," which are not strictly comparable with or homologous to the leaves of dicotyledons. Leaf venation of distinctive pattern has customarily served taxonomists and paleobotanists as an indispensable means of quick recognition of certain plant families, and the presumably parallel venation of monocots as opposed to the reticulate nervation of dicots has been overemphasized and oversimplified. The recent studies of Foster (1950a, 1950b, 1951) on foliar venation in Quiinaceae suggest that much of value may be expected from this field of investigation, but that it is far too early for useful phylogenetic conclusions. The situation appears to have been ably summed up by Foster in the following words (1931, p. 244):

> It seems almost unnecessary to state in these days when all phylogenetic systems are experiencing revision and reexamination in the light of new facts that we are very far from an understanding of the details of foliar evolution.

Although Odell (1932) questioned that even living species could be recognized satisfactorily on the basis of leaf form, venation, and epidermal structure, Edwards (1935) has endorsed the value of cuticular characters, especially in the critical determination of fossil angiosperm leaves, provided a sufficiently broad and detailed comparison is made with living types. An impressive utilization of cuticular and epidermal features in attempting a more natural classification of Gramineae is represented by the studies of Prat (1932, 1936). The so-called "spodogram" technique of Molisch, which consists in revealing the pattern of mineral residues in the epidermis by ashing, has been applied systematically to the Urticales by Bigalke (1933) and to several other groups by Japanese workers.

That the stomata of angiosperms are of diverse types is generally recognized, and Solereder designated four basic kinds in dicotyledons: Ranunculaceous, Cruciferous, Caryophyllaceous, Rubiaceous. Metcalfe and Chalk point out that these types are by no means confined to the families for which they are named, and proposes to substitute new terms for these family designations. Hutchinson believed that the existence of stomatal differences strengthened his fundamental separation of woody and herbaceous lines of dicotyledons. An alignment of Commelinaceae with Gramineae, and of Juncaceae with Cyperaceae, according to Ziegenspeck (1938), is confirmed by stomatal structure. The gratifying results obtained with the phyletic indicator-value of stomata in gymnosperms suggests that further investigation may extend their utility in angiosperms. The preliminary studies of Magnoliales by Rao (1939) and Bondeson (1952) indicate the existence of a diversity of stomatal types in woody Ranales, which may prove of phyletic interest. However, as remarked by Bailey and Nast (1945b, p. 149):

> Not until the stomata of a wide range of the Ranales and other orders have been carefully reinvestigated will it be possible to assess the phylogenetic significance of different stomatal structures in discussions regarding the origin and the relationships of the dicotyledons.

The recent studies by Foster (1944, 1945, 1946) have focussed attention on foliar sclereids as a source of systematic information. A form-classification of these structures has been undertaken by T. A. Rao (1951), who recognizes four principal types based on ontogeny and subdivides them with respect to size and shape. However, as remarked by Foster, "it is hazardous or indeed impossible in many instances to generalize with respect to the major trends in morphological specialization of foliar sclereids within systematic units" (1946, p. 253). Model examples of the successful systematic employment of such foliar characters as shape of midrib xylem, stomata and stomatal crypts, structure of hypodermis, shape of terminal sclereids, and distribution of free sclereids, together with evidence from floral anatomy, are provided by the studies of Morley (1953a, 1953b) on Melastomaceae.

Of a miscellaneous character are the attempts to connect Curcurbitaceae with Passifloraceae by the parallelism of their tendril structures (Hagerup, 1930), Cactaceae with Portulacaceae by similarity in emergences (Chorinsky, 1931), and Julianiaceae to Juglandaceae by their mutual possession of resin canals (Stern, 1952). Although the nature of trichomes is taxonomically useful within a limited frame of reference and some family distinctions are to be noted, even among the monocotyledons (Staudermann, 1924), Heintzelman and Howard assert that at least in Icacinaceae "no broad phylogenetic lines of specialization can be drawn from the study of pubescence" (1948, p. 51). Chattaway (1937) stated that in Sterculiaceae the kind and distribution of crystals in vegetative parts "appear to have little phylogenetic significance" (1937, p. 363).

Inflorescence

The primitive condition of the angiosperm inflorescence has been variously postulated as having been a solitary flower, usually terminal to a leafy shoot (Arber and Parkin, Hallier; Parkin, 1914, 1923; Hutchinson, Sprague, Gunderson), some kind of a panicle (Engler; Zimmerman, 1935; Rickett, 1944), or a dichasial cyme (Woodson, 1936). Croizat (1943) emphatically doubts that either the solitary terminal flower or the cymose raceme is to be regarded as the genesis of all inflorescences. Similarly, both Wettstein and Woodson suggested the solitary-flowered inflorescences are usually derived from pluriflorous ones through reduction, a view expressed by Bailey and his associates in regard to Winteraceae (Nast, 1944; Bailey and Nast, 1945a) and Degeneriaceae (Bailey and Smith, 1942) and by Melchior (1932) with respect to the genus *Viola*. Most authors seem to have agreed that aments, capitula, spikes, umbels, and other compressed or highly branched inflorescences with small flowers are specializations, often showing a combination of aggregation, reduction, and condensation from either angiospermous or gymnospermous ancestors (Arber and Parkin, 1907, 1908; Hallier; Berridge, 1914; Engler; Fisher, 1928; Boothroyd, 1930; Hallock, 1930; Abbe, 1935; Mez, 1936; Manning, 1938, 1940; Abbe and Earle, 1940; Gunderson; Langdon, 1947; Corner, 1949; Stebbins, 1950). Both Parkin (1914) and Engler recognized distinct "cymose" (determinate) and "racemose" (indeterminate) types of flower arrangement. Engler thought both could be derived from a primitive panicle, and Parkin suggested the racemose might have been produced from the cymose by way of a panicle. In Gramineae, Ziegenspeck (1938) advocated the derivation of both the spike and the superfinely branched panicle from a basic panicle, itself perhaps a descendant of the Commelinaceous cincinnus.

In the best available review of inflorescences, Rickett takes a sharply critical view of his subject, finding it impossible to draw clear and meaningful distinctions between "cymose" and "racemose," "simple" and "compound," "axillary" and "terminal" categories, and suggesting that "inflorescences are rarely as simple as they seem" (1914, p. 211). He thinks the simple dichasium may afford at least a starting point for the investigation of inflorescences, and believes that the reduction of individual dichasia and the grouping and shortening of leafy branches bearing them terminally, with the concomitant reduction of leaves to bracts, may afford an explanation for various existing complex arrangements. He concludes that it may be "idle even to speculate on the origin of inflorescences, since we know so little of the relationships of the families of flowering plants, and since by reduction in number of flowers and condensation of branches the same patterns may be attained from different beginnings" (p. 211). This idea of polyphylesis of inflorescences was applied to the "raceme" by Parkin (1914). Woodson, also, has cautioned us (1935, p. 35):

> It would appear a fruitless task to search for the earliest indication of the inflorescence among the extant flowering plants: the origin of the inflorescence is at least as remote as the origin of the flower, and a greater antiquity seems probable from the evidence of paleobotany.

On a more practical level, the separation of Amaryllidaceae from Liliaceae by Hutchinson (1934, 1935) is a classic instance of the utilization of inflorescence characters. Philipson conducted a series of investigations on the capitula or similar structures of Compositae (1946, 1948a), Dipsacaceae (1947a), Valerianaceae (1947b), and Campanulaceae (1948b). On this basis he suggested the fundamental similarity of the Campanulaceous and Composite types, and their basic differences from those of the other two families; that of Dipsacaceae, he thinks, could have been derived from a Caprifoliaceous type.

Floral Morphology and Anatomy

Inasmuch as the classification of angiosperms has, for the past two hundred years, emphasized floral structure, sometimes almost to the exclusion of other features of the plant, it is not surprising that the literature on this subject is appallingly voluminous. Attention will be given here only to those aspects of flowers and flowering which appear to have a fairly direct bearing on problems of classification and phylogeny.

Floral constitution, as it has generally been employed in classification, has been based on the classical morphological interpretation credited to Wolff, Linnaeus, and Goethe and paraphrased by Eames: "The flower morphologically is a determinate stem with appendages, and these appendages are homologous with leaves" (1931, p. 147). As a corollary he adds, "This commonly accepted view of the nature of the flower is sustained by its anatomical structure. Flowers, in their vascular skeletons, differ in no essential way from leafy stems" (p. 147). Granting this classical homology of vegetative shoot and flower, the primitive state of the latter would logically be that most similar to the former. Thus, we might anticipate as primitive a radially symmetrical flower with an elongated axis bearing numerous, indefinite in number, separate, leaflike members arranged in regular spirals, or cycles, or pairs, depending upon the vegetative phyllotaxy. Such an archetypic flower would possess essentially that central floral plan from which de Candolle regarded all other kinds as derivative in consequence of cohesion, adnation, abortion, or change of symmetry. It is also essentially the *euanthium* (*euanthostrobilus*) of those numerous authors who have thought the primitive flower to be a simple bisexual strobilus, perhaps best represented among living forms by apocarpus, entomophilous, hypogynous Ranales (Polycarpicae) of the dicotyledons and Alismatales (Helobiae) of the monocotyledons. Even those who have regarded some other basic floral type as more archaic, or who have accepted a polyphyletic origin of angiosperms, have usually held the Ranalian flower to be the prototype of some or most other flowering plants. Perhaps it should be emphasized at this juncture that Arber and Parkin cautioned: "As we have pointed out, there is no reason to believe that any Angiosperm with a complete assemblage of primitive floral characters is to be found today, nor indeed that such a flower ever existed" (1907, p. 45). Rather, the presumed ancestral traits are to be discovered dispersed among existing dicotyledons and monocotyledons, especially Ranales.

The principal dissent from the acceptance of the "complete" hermaphrodite flower as primitive initially came from those who, following Eichler, Engler, and Wettstein, attempted to find homologies between unisexual gymnospermous inflorescences or strobili of vascular cryptogams and a wind-pollinated, unisexual flower with little or no floral envelope (*pseudanthium*). According to Engler, "it is especially not to be conceded that families with prevalently wind-pollinated plants without any or only simple perianths could have developed from insect-flowers with simple or double perianth" (p. xxiii). The difficulties in the way of manufacturing a bisexual flower from unisexual inflorescences or strobili (Karsten, Vuillemin, Neumayer, Wettstein, Emberger) or of an angiospermous gynoecium from naked ovules or sporangia (Thomas, Hagerup, Hjelmqvist, Janchen), has led to the spinning of ingenious but tortured "character-phylogenies" which strain credulity. Calestani (1933) has raised the interesting suggestion that the ancestral angiosperms must have been entomophilous and bisexual in order to have had a selective advantage over the anemophilous, unisexual gymnosperms.

In recent years, there have been numerous attempts to explain the structure of angiosperm flowers on the basis of the features of Devonian Psilophytes, assuming that all the organs of vascular plants are referable to aggregations of fertile and sterile "telomes" (Zimmermann; Thomas, 1934, 1936; Hunt; Chadefaud, 1946, 1947; Bertrand, 1947a; Lam; van der Hammen, 1948; Emberger, 1950, 1951; Wilson; Suessenguth and Merxmüller, 1952; Takhtajan, 1953). To this entire group of proposals, Arber's pithy comment on Zimmermann's "*Merkmalsphylogenie*" is equally pertinent. She characterized his approach as "relatively confused and incoherent—an inevitable result of the attempt to fit the facts of floral structure into a scheme based upon the organization of a group with which it may well be that the forbears of the angiosperms never had any connection" (1937, p. 178).

Far more serious has been the challenge hurled by those who, on the basis of physiological and ontogenetic processes, have called into question the basic homology of flowers with vegetative shoots and of floral and foliar structures. Thompson (1935, 1944), rebelling against the formalism of the classical concept, argued that a flower is primarily a "sporogenous axis" bearing emergences, and that it is in no way comparable with a leafy shoot; Belin-Milleron (1951) echoes this view, and Philipson (1949) seems to give it some support. Grégoire (1931, 1938) maintained that reproductive and vegetative apices, because of their organization and relationship to the plant body, the mode of development of the procambium, and the origin of their appendages, are "irreducible" entities. This position has been supplemented with evidence from phyllotaxy by Plantefol (1947, 1949), who thought that only the sepals possessed homology with foliage leaves. (Some of these ideas have been reviewed by Bancroft, 1935; Kozo-Poljanski, 1936; Arber, 1937; Foster, 1939; Troll, 1939a; Unruh, 1939; Wilson and Just, 1939; Matthews, 1941; Watson; Ozenda, 1946, 1949; Joshi, 1947; Philipson, 1949; Kasapligil, 1951; and Tepfer, 1953.) Working with periclinal chimeras, Satina and Blakeslee (1941, 1943) have drawn the inference that sepals and petals are truly foliar, but that stamens and carpels are not because of their initiation in less superficial cell layers.

Those who have read a peltate organization into some foliage leaves and most floral organs, have found in this conception further grounds for maintaining the basic homology of these structures (Troll, 1927, 1932, 1934, 1939a, 1939b; Schaeppi, 1936, 1939; Kaussmann, 1941; Leinfellner, 1950, 1951; Baum, 1950).

By assuming that vascular tissues are slower to undergo cohesion, adnation, or abortion than are the organs they supply, it becomes possible through anatomical investigation to detect the phylogenetically earlier condition of a specialized flower (C. V. Rao, 1951). This idea of conservatism of the vascular tissues has been emphasized particularly by Saunders (1937–1939, 1939) and by Eames (1926, 1931) and his students. Saunders, indeed, carried this principle so far as to attribute virtual independence to every floral trace, especially of the gynoecium, a position which Eames has attacked vigorously. Puri (1951, 1952a, 1952b, 1952c) describes an hypothetical standard flower as one which is pentacyclic (two perianth whorls, two staminal, one carpellary), each whorl receiving distinct vascular bundles from the stele. Each sepal would receive three, each petal one, each stamen one, and each carpel three; in this skeletally primitive flower there would be no cohesion or adnation of these bundles. Although Arber scolds such usage of "floral anatomy . . . as a reliquary to be rifled for 'ancestral traits' " (1933, p. 240), and numerous authors have shown that the vascular supply may be less, more, or equally persistent than the organ itself (Smith, 1926; Eggers, 1935), there seems little doubt that vestigial vasculation may sometimes afford phylogenetically valuable evidence. This approach has now been applied to members of many orders with the objective of clarifying floral structure and often of improving classification thereby, viz., Ranales (Smith, 1926; Rassner, 1931; Schöffel, 1932; Brouland, 1935; Chapman, 1936; Reece, 1939; Kasapligil; Tepfer), Rhoedales (Eggers; Norris, 1941; Stoudt, 1941), Malvales (C. V. Rao, 1952), Geraniales (Moore, 1936b), Caryophyllales (Laubengayer, 1937; Mattfeld, 1938a, 1938b; Thomson, 1942), Ericales (Copeland, 1935b, 1937, 1938, 1939, 1941, 1943, 1947; Palser, 1951; Chou, 1952), Primulales (Dickson, 1936; Douglas, 1936), Gentianales (Lindsey, 1938, 1940; Woodson and Moore, 1938), Polemoniales (Copeland, 1935a; Dawson, 1936; Lawrence, 1937), Rosales (Jackson, 1934; Moore, 1936a), Rubiales (Wilkinson, 1949), and Asterales (Koch, 1930), and such distinctive families as Proteaceae (Kausik 1938a, 1938b) and Thymelacaceae (Leandri, 1930; Heinig, 1951).

A. *Perianth:* A wide variety of explanations has been offered as to the origin and primitive constitution of the perianth. That a sterile perianth, well differentiated from both foliage leaves and sporophylls, was present in the first angiosperms was postulated by Arber and Parkin, Wernham (1911–1912), and Bessey. It has been suggested that the dicot perianth was initially divisible into calyx and corolla (Hutchinson; Stebbins, 1951), and that it was not (Hallier, Bessey, Gunderson). Glück (1919), following Prantl, supposed the whole perianth to be derived from foliar bracts, while Worsdell (1903, 1907) metamorphosed the perianth *in toto* from the androecium. More popular, however, has been the alternative of obtaining sepals through modification of bracteoles, and petals by sterilization of stamens, with which they usually agree in possessing a single trace (Rendle, 1903; Engler; Smith, 1926; Troll, 1939a; Eames, Wettstein). To Sprague, "the hypothesis of a single primitive type of perianth seems superfluous" (1925, p. 113), a view in which he has been joined by Arber and Parkin, Mattfeld, Ehrenbergh (1945) and, I suspect, many modern workers. Much has been made of the fact that Alismatales possess a heterogeneous floral envelope like that of most dicots, whereas that of most other monocots is homogeneous and hence allegedly derived wholly from androecium (Nicotra, 1909–1910; Salisbury, Hutchinson; Eber, 1934; Markgraf, 1936). On the contrary Glück and Plantefol viewed the entire monocotyledonous perianth as foliar, the latter on phyllotactic grounds; Puri (1951) regards it as composed wholly of "tepals." Attention should perhaps be called to the anomalous genus *Trimenia*, where bracteoles intergrade to tepals (Money, Bailey and Swamy, 1950), and to Winteraceae, where the primitive calyx is synsepalous although the numerous petals are free (Bailey and Nast, 1945a). In Caprifoliaceae, even within the same genus, the vascular supply of a sepal may be reduced from three traces to one (Wilkinson, 1949). Mattfield (1938a, 1938b) derived the petals in Caryophyllaceae and other families from the adaxially fused stipules of the alternisepalous stamens. Woodson and Moore (1938) interpreted both calycine and coralline scales in Apocynaceae as stipular; Heinig (1951) thinks the petaloid scales in Thymelaeaceae possibly represent sepalar stipules, whereas Leandri (1930) apparently considered them abortive petals.

Once a double perianth has been formed, however, there is a rather general consensus that the principal trends of evolution are from spiral to cyclic arrangement, hypogynous or perigynous to epigynous, pentacyclic to tetracyclic, polymerous to oligomerous, choripetalous to sympetalous, and actinomorphic to zygomorphic. These modifications are customarily visualized as owing to adaptation to the demands of pollinators (Thomas, 1931; Stebbins, 1951), whether insects (Robertson, 1904; Worsdell; Ames, 1937, 1946; Pennell, 1948; Grant, 1949, 1950a, 1950b, 1950c, 1952; Li, 1951), birds (Porsch, 1931, 1932, 1933), or even bats (Porsch, 1934-1935, 1937, 1942). Conversely, reduction in all floral structures may arise as a consequence of a change to anemophily (Wirth, 1923; Fagerlind, 1948; Porsch, 1950; and cf. "Amentiferae," below).

B. *Androecium:* The general homogeneity of staminal structure is, according to Parkin, one of the principal arguments for the monophylesis of angiosperms. This uniformity does not, however, extend to the attempted explanations of the origin and morphological homologies of stamens, as might be anticipated from the conflicting concepts of the flower mentioned above. The stamens have frequently been interpreted as cauline structures, representing: (1) the axes of male flowers (Neumayer, 1924); (2) the condensation products of dichotomously branched systems bearing terminal fertile "telomes" (Thomas; Wilson, 1937, 1941, 1942, 1950; Reece, Bertrand, Emberger); and (3) the sporogeneous emergences from a "staminal ring" (Plantefol). Ehrenberg (1945) has suggested that tepals and stamens spring from tangential division of the same primordia.

The classical view that stamens are "phyllomes," homologous with leaves, has been more generally accepted (Arber and Parkin, Hallier, Bessey, Eames, Troll; Schaeppi, 1939; Gunderson; Baum, 1949c; Parkin, 1951; Ozenda, 1952). Of special significance to this latter view is the work of Bailey and his associates in calling attention to the occurrence of broad, microsporophyll-like stamens in more than a dozen families of the Ranales (Bailey and Smith; Bailey and Nast, 1943a, 1945a; Bailey, Nast and Smith, 1943; Bailey, 1949; Bailey and Swamy, 1949; Canright, 1952). These stamens are characterized by a three-trace vasculation, elongate linear sporangia embedded in tissue of the sporophyll, and the lack of any clear division into filament, connective, and anther. Canright regards the stamen of *Degeneria* as the closest living epitome of the primitive angiosperm stamen, and gives a synopsis of trends of specialization in staminal form occurring within Magnoliaceae. This reviewer finds no difficulty in accepting the last author's conclusion that,

> . . . the preponderance of evidence seems to support the hypothesis that these broad types of microsporophylls are primitive and, as such, should be considered as relatively unmodified phyllomes. With this concept in mind, the conventional stamen with its narrow filament and protuberant terminal anther should be recognized as an extreme specialization of this primitive type of microsporophyll (Canright, 1952, p. 487).

Evolutionary trends from spiral or hemicyclic to cyclic arrangement, from two whorls to a single whorl, from numerous to few members per whorl, from free to connate, from hypogynous or perigynous to epipetalous or epigynous, from tetrasporangiate to bisporangiate, and from longitudinally to poricidally dehiscent, are generally accepted. The distinction between the usual centripetal development of stamens and their centrifugal maturation in orders centering around the Parietales is regarded by Corner (1946) as of systematic importance. Effective classificatory use of characters of the androecium has been made in such groups as Ericales (Matthews and Knox, 1926; Matthews and MacLachlan, 1929; Copeland; Doyel and Goss, 1941; Palser, 1951; Kavaljian, 1952), Malvales (Edlin, 1935; C. V. Rao, 1952), and Melastomaceae (Morley).

C. Gynoecium: The classical interpretation of the carpel, dating at least from de Candolle, regards this organ as an infolded, leaflike structure with its margins more or less fused and bearing ovules. Arber and Parkin made the explicit statement: "We regard the carpel as a megasporophyll, present in the ancestor of the Angiosperms as an open leaf, bearing several ovules on its margins, and not unlike the megasporophyll of *Cycas*" (1907, p. 47). Chadefaud (1936) would derive the angiosperm carpel directly from a cycadean sporophyll, and Thomas at one time (1931) visualized the evolution of a Ranalian follicle from a Seed Fern sporophyll by way of a Caytonialian fructification as an intermediate stage. (Hirmer [1935] and Harris [1940, 1951a, 1951b] have contended that Caytoniales are themselves Seed Ferns with clearly gymnospermous pollination, and hence that their structures are only analogous with those of angiosperms.) The basic angiosperm carpel is usually regarded as having been a few- or many-ovuled follicle with three vascular traces—one dorsal and two lateral—although Fraser (1937) thought there might have been five originally. Carpels were interpreted as peltate organs homologous with peltate leaves by Troll (1932, 1934, 1939b), Eber, Schaeppi (1936), Leinfellner (1940, 1950, 1951), Sprotte (1940), and Baum (1948, 1949a, 1949b); only a few families of Alismatales were credited with having epeltate ones.

The fact that it is the last-formed and often an ostensibly terminal structure of the floral axis, frequently with a complex vasculation, has caused the gynoecium to be visualized also as a complex largely of cauline origin. It has been variously suggested: (1) that the carpels or the gynoecium are in all or in some angiosperms "emergences" of an axillary or cauline nature without foliar homologies (Thompson, Grégoire, Satina and Blakeslee; Philipson, 1949; Plantefol); (2) that the gynoecium is a mixture of cauline and foliar elements, with the cauline complement decreasing (Vuillemin, 1919; Neumayer) or increasing (Ozenda) with evolutionary advance; (3) that the ovules were originally borne naked on cauline placentae, the envelopment of which by a cupule or a whorl of bracts has resulted in angiospermy (Wettstein, Thomas; Hagerup, 1938, 1942; Langdon, 1939); and (4) that the carpels are formed from condensed dichotomous branch-systems, either directly, or indirectly by way of "foliarized" branch-systems homologous with foliage leaves (Zimmerman, Hunt, Emberger). The division of gymnospermous sporangia into "phyllosporous" and "stachysporous" by Sahni, has been extended to angiosperms with the assumption of at least a diphyletic origin and the recognition of one line bearing ovules on sporophylls (most angiosperms) and the other bearing them on cauline structures ("Amentiferae," Caryophyllales, possibly Primulales) (Lam, 1948a, 1948b, 1950, 1952; Suessenguth and Merxmüller). This suggestion is particularly noteworthy when it is stated that the two conditions have been distinct since the Devonian, and yet that the androecium may be "phyllosporous" and the gynoecium "stachysporous" in the same flower! After undertaking a broad if superficial survey of angiospermous material, van der Hammen concluded: "It provisionally seems that the distribution of phyllospory and stachyspory in the Angiosperms is more intricate than was originally conceived" (1948, p. 298).

Considerably more promising is the discovery by Bailey and his co-workers of the existence within woody Ranales of apparently primitive, stipitate, conduplicate, three-veined, styleless, unsealed carpels, bearing two independent external stigmatic crests and two rows of ovules attached between and vascularized by the midvein and the two lateral veins (Bailey and Smith; Bailey and Nast, 1943b, 1945a; Nast and Bailey, 1945, 1946; Bailey, 1949; Bailey and Swamy, 1951). It is remarked that, "the classical concept of an involute carpel with marginal placentation and a localized apical stigmatic surface will have to be modified" (Bailey and Swamy, 1951, p. 379), but the necessary emendation appears to be a relatively slight one, and the discovery has put the tenet of the foliar homology of the carpel in an extremely enviable position (Just, 1952).

The biological significance of the enclosure of ovules has usually been regarded in terms of better protection of the ovules (Grant, 1950b; Mangenot, 1952) or of increasing the efficacy of insect pollination (Arber and Parkin, Robertson). However, Whitehouse has substituted an intriguing genetical hypothesis (1950, p. 215):

> It is suggested that multiple-allelomorphic incompatibility of pollen and carpel tissue has been the primary cause of the evolution of the closed carpel and of the success of the angiosperms over their gymnospermous ancestors. The profound significance of the closed carpel for angiosperm evolution would then lie in the protection of the ovules, not from desiccation or the attacks of animals, but from fertilization by the individual's own pollen, without appreciably restricting cross-fertilization.

Phylogenetic trends in gynoecia from spiral to cyclic, from apocarpy to syncarpy, from numerous and indefinite parts to few and of mixed number, from polyovulate to uniovulate, from superior to inferior, are generally acknowledged. Reduction may sometimes go beyond the bicarpellate stage, with degeneration of one of the carpels (Wilkinson), or to a secondarily simple or "pseudomonomerous" condition (Eckhardt, 1937, 1938), or even to one approaching a gymnospermous appearance (Fagerlind, 1948). With syncarpy, further complications and controversies arise. Saunders (1937–1939) believed that, on the basis of vasculation, a syncarpous gynoecium was composed of two alternating whorls of sterile and fertile carpels—her theory of carpel polymorphism, which has received a great deal of discussion but won few adherents. Floral anatomy has been used by Douglas (1944; cf. also Egler, 1951) to indicate that the outer tissies of the inferior ovary are usually appendicular, as they appear to be in *Begonia* (Gauthier, 1950), but Puri (1951, 1952a, 1952c) doubts that this problem is fully settled. Thompson has maintained that the inferior ovary is strictly a receptacular, acarpous structure, and Leinfellner (1941) that it is axial externally, purely carpellary in the interior. In his interesting quasiphysiological discussion of the flower, Schaffner (1937) stressed three trends (which he believed to be orthogenetic) toward determinate growth, expansive growth resulting in the production of disks and hypanthia, and intercalary growth between androecium and gynoecium. These developments are not, perhaps, very different from those which Stebbins (1950) credits to allometry, comprising a shift to zonal or toral growth, or from successive to simultaneous, developments which have played such an important role in producing floral diversity.

The importance of placentation for taxonomic purposes has been appreciated since the time of Lindley, but there appears to be little agreement with regard to it otherwise. In the latest review of the subject I have found, Puri (1952b), emphasizing vasculation, recognizes some eight conditions of ovule attachment in angiosperms. He apparently is inclined to regard the axile condition, in syncarpous gynoecia, as fundamental, and parietal, free-central, and basal as derivative. Winkler (1939) held similar views, but pointed out that false septa might arise almost anywhere; in Malvales C. V. Rao (1952) postulates multiplication of carpels by "chorisis," while Edlin thought the free carpels secondarily derived from a syncarpous condition. Free-central placentation—one of the chief props of "stachyspory"—is now generally conceded to be a reduction product from axile placentation in both Caryophyllales (Laubengayer, Thomson) and Primulales (Dickson, Douglas), constituting a bond of affinity between the two groups. Gunderson (1939a, 1939b, 1941, 1943), apparently chiefly on ontogenetic grounds, thought that carpels united first by their margins, and hence that parietal placentation is primitive. Axile placentation, achieved by extension of the placentae to, and their union at, the center of the gynoecium, he regarded as an evolutionary advance, providing the ovules with better nourishment and protection. He also suggested that one or few ovules with basal placentation is a condition associated with anemophily, that numerous ovules located parietally indicate entomophily, and that both conditions may be primitive. Perhaps in Gentianaceae (Lindsey) and Begoniaceae (Gauthier) parietal placentation preceded axile and in Cactaceae (Buxbaum, 1944) free-central. Troll 1933a, 1933b) and Leinfellner (1950) drew a sharp distinction between a "syncarpous" ("eusyncarpous")—multilocular with axile placentation—and a "paracarpous" ("hemisyncarpous")—unilocular with parietal or free-central placentation—gynoecium and found them to be quite different in their vertical organization. However, Eames avers that "lines between types of placentation do not exist" (1951, p. 23). Puri is uncertain as to the origin of laminar placentation, but many have found it important in linking the monocotyledonous Alismatales with Nymphaeaceae, and Junell (1934) regarded it as the placentation type basic to Viticoideae (Verbenaceae) and all Labiatae, including those members of the latter family which have dry nutlets and a gynobasic style. Blaser (1941) distinguished Cyperaceae from Gramineae by the fact that, while both have solitary basal ovules, those of the former are derived from free-central placentation, those of the latter from parietal. It may be significant that in Ranales incipient syncarpy has arisen in at least three ways (Bailey and Swamy, 1951), and one is inclined to agree with Puri that "it is apparent that there is no uniform pattern followed and evolution seems to have progressed along several lines" (1952b, p. 625).

D. *Nectaries:* Because the angiosperms are believed by many to have been primitively insect-pollinated, it has been suggested that they were also basically honey producers (Nicotra; Werth, 1923). As early as 1913, Porsch was calling attention to the possible utility of nectaries as indicators of phylogenetic relationship, but it was Brown (1938) who really took this suggestion seriously. Brown warned that nectaries appear to have arisen independently in different lines of affinity, and that they have then undergone modifications characteristic of the various groups. Basing his groupings on the Hutchinson (1926) system and emphasizing woody versus herbaceous lines, he recognized five principal nectarine plexi: (1) septal, or ovarial glands, confined to monocotyledons, in which he thought palms might be primitive; (2) gynoecial, androecial, or toral disk nectaries, centering about Theales or Bixales (Guttiferales), and leading in several directions—through the Sympetalae to Lamiales, to herbaceous Caryophyllales, and to Rhoedales and perhaps Salicales; (3) cushion-nectaries, confined to Malvales; (4) toral disk nectaries, leading from perigynous Rosales to the epigynous Compositae by one sequence and to Myrtales by another; and (5) staminal nectaries, in higher Ranales. Several authors (Werth, 1941; Jaeger, 1950) have emphasized the diversity of Ranalian nectaries as confirming the central position of this order phylogenetically, and thus as affording a connecting link between dicots and monocots (Porsch, 1913).

It is generally assumed that, although there may be a well-defined trend from foliar to disk or toral nectaries in dicotyledons, nectaries may also have been contrived from any suitable material at hand—vestigial perianth (Fisher), staminodia (Daumann, 1931a, 1931b; Dawson; Moore, 1936a; Mattfeld) or abortive carpels (Woodson and Moore). The doctrine of vascular conservatism has frequently been called into play to decipher their derivation (Kausik, Kasapligil). Fahn (1952) has recently undertaken a morphological-topographical classification, and recognizes the Torus, Perigonal, Stamen, Ovarial, and Stylar types. Although Brown has pointed to the lack of nectaries in Magnoliales (Ranales), Calestani and others have emphasized the secretion of nectar by stigma and style in this group. Both Norris and Stoudt employed nectarine characters in tracing affinity among the constituent families of Rhoedales. Benson (1940) has stressed the different kinds of nectary scales in *Ranunculus,* and has used them taxonomically. Werth (1923) suggested a degradation series from entomophilous to anemophilous flowers, in which nectaries shift from a foliar to an axial position, followed by complete loss of nectaries with the attainment of unisexuality and wind-pollination. A survey of extrafloral nectaries was undertaken by Zimmermann (1932) but he concluded that these structures were determined physiologically and ecologically, and had little or no phyletic significance.

Embryology

Comparative or systematic embryology, comprising particularly the features of the ovule and the female and male gametophytes, has received serious attention only during the last half-century, according to Maheshwari (1945), greatly stimulated by the work of Schnarf (1931, 1933, 1936, 1937b). Both these authors have expressed the belief that such internal characters should be more conservative than others more exposed to external influences, and hence should be of significance in systematic and phylogenetic endeavors.

A. *Ovule:* The nature and homologies of the angiosperm ovule have been fully as vexed a question as has the morphological value of the carpel, and the widely varying interpretations of the two structures are closely interrelated. Those who have read into the angiospermous gynoecium axial, soral, cupular, or telomic origins, or "involutions," usually with the construction of ingenuous typological seriations, do not seem to have advanced greatly our understanding of ovule structure (cf. de Haan, 1920; Neumayer, Wettstein; Appl, 1939; Unruh; Hagerup, 1942; Chadefaud, 1946; Ozenda, 1946; Bertrand, 1947a; Martens, 1947, 1951; Fagerlind, 1948; Just, 1948; Emberger, 1949, 1950, 1951; Mangenot; Walton, 1952). Although a direct relationship between the constitution of the ovules of angiosperms and that of the ovule of any particular group of gymnosperms is not wholly clear, there seems to be rather general agreement that at least all angiosperm ovules are essentially homologous, if we disregard the extremist views of "acarpy" and of "phyllospory-stachyspory." For our purposes the ovule may be defined as a megasporangium consisting of a nucellus surrounded by one or two integuments, of uncertain origin. Within the nucellus develops an archesporium which ultimately gives rise via megaspore mother cells to a female gametophyte. Although disagreements as to different features remain, some idea of the characteristics which have been regarded as primitive for angiosperm ovules may be culled from the voluminous literature. Several types of ovule, based on the orientation of micropyle in relation to ovule-attachment are recognized. Earlier, the orthotropous or atropous type (Arber and Parkin, Engler), but more recently, the anatropous (Parkin, 1923; Netolitzky, 1926), has been regarded as primitive. It may be of significance that the ovules borne in unspecialized Ranalian carpels appear to be largely anatropous (Bailey and Swamy, 1951). Nitzschke (1914) and Salisbury have stressed that the ovules of Alismatales and Nymphaeaceae are anatropous. In Malvales, Reeves (1936) has postulated the origin of anatropous from campylotropous ovules by relegation of the curvature of the ovule to its funiculus.

The presence of two integuments, each usually consisting of more than a single layer of cells, is generally regarded as primitive (Arber and Parkin, Hallier, Engler, Netolitzky, Sporne). The possession of a single massive integument by most Sympetalae has been generally accepted as representing an evolutionary advance, and has led Copeland (1935a), almost alone, to defend this group as a truly monophyletic one. Hallock (1930) called attention to the occurrence of a similar, single integument in *Garrya* as a sign of advancement. All but one genus of palms, according to Bosch (1947), have anatropous ovules with the two integuments fused together. The presence of vascular bundles in the ovule, more particularly in the integuments, has been stressed as an archaic feature (Zimmermann, Sporne; Janchen, 1950; Walton), but Kühn (1928), after a broad survey of families, concluded that this development is polyphyletic. Bailey and Nast (1945b) have described the occurrence of a vascularized subchalazal projection of the ovules of *Trochodendron* and *Tetracentron* as being unique among angiosperms and perhaps an indication of primitiveness. There appears to be in vascular plants a tendency for the steadily increasing envelopment and protection of the female reproductive apparatus, and the angiosperm ovule may be visualized as the climax of this trend (Emberger, 1950; Grant, 1950b; Mangenot), with the loss of integuments and vascularization as an associated phenomenon. Fagerlind (1948) attempted to trace a reduction series within Santalales, which commences with an ovule provided with two integuments and culminates in a highly reduced, naked, nucellus-like ovule. Some weight has been given, also, to the degree of fusion between inner integument and nucellus: an attachment only at the apex, often with cuticular developments of the intervening surfaces, may represent a primitive condition (Netolitzky, Kausik, Hjelmqvist). The possession of a massive nucellus which affords the principal food supply for the developing embryo sac, is assumed to be an original feature (Nitzschke, Hallier, Netolitzky; Fagerlind, 1948). To Engler, the development of the nucellus was more important than persistence of the integument. A reduction series in size of nucellus was postulated by Nitzschke (1914), connecting Nymphaeaceae and Alismataceae. The existence of a several-celled archesporium, because *Casuarina* shows this peculiarity, has been made much of by those seeking to establish a close connection between gymnosperms and "the Amentiferae" (Engler, Zimmermann, Hjelmqvist), but faith in its evolutionary significance appears to have declined (Maheshwari, 1950).

The mode of development within the ovule and the entrance into the female gametophyte of the pollen tube, whether endotropic and chalazogamous or ectotropic and porogamous, has been accorded major importance in the past. Indeed, Engler's initial placing of *Casuarina* at the very beginning of the dicotyledons was largely based on the belief that chalazogamy is a primitive feature affording unquestionable relationship between higher gymnosperms and "the Amentiferae," a view supported at least in part by K. Fritsch (1905), Wettstein, Zimmermann, Hjelmqvist, Janchen, and Suessenguth and Merxmüller. The subsequent discovery that chalazogamy occurs sporadically in various groups of angiosperms, and that the course of pollen-tube growth appears to be determined physiologically rather than phylogenetically, has resulted in considerable deemphasis (Maheshwari, 1950).

B. *Female gametophyte:* While these and other features of the ovule have been drawn upon for taxonomic and phylogenetic purposes, the focus of attention has long been upon the female gametophyte. "The origin of the embryo sac remains today," as recently affirmed by Battaglia, "one of the outstanding problems of Angiosperm evolution" (1951, p. 87). The several interpretations extant seek to explain the angiosperm structure by derivation from the archegonia-bearing female gametophyte of gymnosperms. The discovery of Hofmeister and Strasburger of striking resemblances between the gametophytes of some Gnetales—two genera of which likewise lack archegonia—and those of flowering plants was interpreted as a confirmation of the phylogenetic views of Engler and Wettstein. Battaglia, in proposing his "Archegonial Disappearance Theory," states that "an archegonial homology between angiosperms and gymnosperms does not exist" (1951, p. 90), and he, Schnarf, and Maheshwari agree in regarding the situation in Gnetales as merely parallel with, and not genetically related to, that prevailing in angiosperms.

The uniformity of mature embryo-sac structure in angiosperms has been widely offered as a compelling argument for their monophyletic origin (Bessey, Sargant, Parkin, Schnarf; Maheshwari, 1939; Copeland, 1940; Fagerlind, 1946; Johansen, 1950; Whitehouse). Joshi (1938), Turrill (1942), and Gaussen (1952), however, have interpreted the occurrence of embryo sacs of different development and ultimate configuration as evidence suggesting polyphylesis of the group. Some ten different (sexual) embryo-sac types are distinguishable on the basis of the number of megaspores from which they take their origin (mono-, bi-, or tetrasporic), the number of cell or nuclear divisions intervening between initiation and maturity, and the number and arrangement of component cells or nuclei when fully formed (Maheshwari, 1937, 1945, 1948, 1950; Battaglia). That the monosporic, eight-nucleate Normal or Polygonum type is primitive for the angiosperms has been generally maintained, because it has the largest number of nuclear divisions, spore formation and embryo-sac development are well separated temporally, it is the most common type—in some 70 per cent of angiosperms thus far investigated, according to Maheshwari—and because all other types can be derived from it (Sargant, Lotsy, Parkin, Engler, Schnarf, Copeland, Maheshwari, Battaglia). Unfortunately for purposes of classification and evolutionary interpretation, the distribution of embryo-sac types appears to be largely haphazard, although Fagerlind (1944) supposes tetrasporic gametophytes to be indicative of relationships within at least some taxa. The shining exception is the restriction of the *Oenothera* type (monosporic, four-nucleate) to Onagraceae; this phenomenon permits expulsion from the family of the anomalous genus *Trapa,* which has an eight-nucleate embryo sac and other structural peculiarities. The genus *Calochortus,* according to Cave (1941), should be excluded from Tulipae and Lilioideae because of its lack of a *Fritillaria*-type embryo sac and certain characteristics in chromosome number. Suessenguth (1921) and Salisbury found in embryo-sac features a further verification of a connection between Ranales and Alismatales; the importance of a multinucleate embryo sac as indicating relationship between Piperales and Arales or Pandanaceae, is denied by Maheshwari (1950).

The explanation of "double fertilization" and the homologies of the polyploid endosperm have generated a great deal of discussion and widely different opinions. The occurrence of a "double fertilization," together with the general uniformity of other features of the ovule and particularly the embryo sac, has been given the greatest importance as providing conclusive evidence that angiosperms have had a single basis (Sargant, Schnarf, Fagerlind, Whitehouse; Parkin, 1952). However, Battaglia believes that the antipodals and the polar (proendospermatic) cell are actually latent primary-endosperm initials awaiting physiological stimulus, and that "double fertilization" is a misnomer for the necessary stimulation furnished by mitosis. *"Polyantipody, in the phylogeny of angiosperms, should, therefore, be an indication of primitiveness"* (1951, p. 96). Brink and Cooper (1940) have stressed that "double fertilization" gives the embryo the advantage of a rapidly developing food supply through polyploid heterosis. Glišić (1929) used features of the endosperm and haustorial similarities to relate Orobanchaceae closely to Scrophulariaceae, and Campbell (1930a) shifted *Paulownia* from Scrophulariaceae to Bignoniaceae despite differences in endosperm.

C. *Male gametophyte:* The male gametophyte of angiosperms is the germinated pollen grain with its fully developed pollen tube. Although it is generally assumed to have been derived, with a further reduction of prothallial tissue, from some ancestral gymnosperm, we know very little about either its origin or its subsequent evolution (Maheshwari, 1949, 1950; Battaglia). Because of the important role now being played by microfossils in the comparative dating of phytogeographical, climatological, and archeological events, there is currently a great deal of interest in pollen and palynology. The importance of fresh pollen in allergy, also, has led to the accumulation of the kind of comparative data required for systematic purposes. The features of the stamen and the male gametophyte commonly accepted as of classificatory value include: (1) the nature of the anther tapetum, whether glandular or plasmodial; (2) the mode of division (simultaneous or successive) of the microspore mother cells and the resultant configuration of the spore tetrads; and (3) the morphology of the pollen grain, comprising particularly size, shape, and symmetry, the number and position of apertures (germ pores) and furrows (colpae), the adornment of the outer spore wall (exine, sporoderm), the number of nuclei in the pollen grain at the time of spore discharge, and whether the grains are borne singly, or cohere in tetrads or pollinia (Engler; Wodehouse, 1928, 1935; Tischler, 1929; Schnarf, 1931, 1933, 1937b; Maheshwari 1945, 1949, 1950; Erdtman, 1953). The modes of origin of the tapetum were utilized by P. Clausen (1927) to confirm relationship between Alismatales and Ranales. In general, dicotyledons have a simultaneous division of microspore mother cells resulting in tetrahedrally arranged tetrads of spores, whereas monocotyledons show successive divisions producing a non-tetrahedral conformation (Erdtman, 1943), but deviations in this rule appear to show affinity between Alismatales and Ranales (Suessenguth). Whether the pollen grain contains two or three nuclei when shed has been used to recommend the exclusion of Heliotropioideae from Boraginaceae (Schnarf, 1937a) and taxonomically within Labiatae (Leitner, 1942).

Assumptions of affinity based on such individual characters should be judged in the light of facts that a single pollen feature or type may be widespread in related or even unrelated groups, that even closely allied groups may show great discrepancies in microspore characteristics, and that convergences and parallelism are as frequent and confusing here as in other structures (Wodehouse, 1928, 1935; Pope, 1925; Erdtman, 1953). Consequently, indications of affinity are doubtless more reliable if based on a spectrum of pollen characters, such as embodied in the *palynogram* of Erdtman (1953), or correlated with other aspects of plant structure (Heimsch, 1940; Hedberg, 1946; Dahl, 1952). Pollen features have been used to relate *Rhoiptelea* to Juglandaceae (Withner), to re-align members of Liliaceae and Amaryllidaceae (Wunderlich, 1936), to assign genera of uncertain affinity within Sterculiaceae (C. V. Rao, 1950), to underline a connection between Myristicaceae and Annonaceae (Joshi, 1946), and to clarify relationships in Ericales (Copeland, Doyel and Goss, Kavaljian). The degeneration of three microspores of the tetrad in Cyperaceae has been suggested as adding to the distinctness of that family, while at the same time relating it to Juncaceae and separating it from Gramineae (Engler; Wulff, 1939; Wahl, 1940; Maheshwari, 1949). Considerable attention has been paid to size of pollen within a restricted group as an indicator of polyploid level (Erlanson, 1931, 1934), but it is also clear that this approach must be employed with caution (Bell, 1954). The occurrence of dimorphic pollen in the same taxon of heterostylic plants (Baker, 1948) has long been known, and Johnston (1952) finds two basically different types of grain in *Lithospermum*, a feature which he turns to advantage taxonomically.

Perhaps the most important data of phylogenetic significance emerge from the distribution of the single-furrowed type of grain, which is characteristic of Seed Ferns, Bennettitales, Cycadales, Ginkgoales, and most monocotyledons. Hallier regarded this type and the occurrence of permanent tetrads as primitive in angiosperms. Although the dicots normally have tricolpate pollen (or modifications thereof), there are now known some twenty groups of dicots with the basic monocolpate pollen (or such derived forms of it as are found in *Trimenia* and some Chloranthaceae, Nymphaeaceae, Cabombaceae)—all of them in the Ranales (Hallier; Pohl, 1928; Wodehouse, 1936a; Bailey and Nast, 1943a, 1945a, 1948; Bailey, 1949; Money, Bailey and Swamy; Canright). The Ranales, then, are the sole group of angiosperms known to have both monocolpate and tricolpate pollen, the retention of the former presumably being an archaic character.

Winteraceae are remarkable for the retention of the one-pored grains in a permanent tetrad (Bailey and Nast, 1943a, 1945a), a characteristic which Robertson believed to be linked with insect pollination. The pollen of *Euptelea* fluctuates between monocolpate and tricolpate, as does that of some members of Ranunculaceae and Berberidaceae (Nast and Bailey, 1946). In view of the frequently suggested affinity between Ranales and Alismatales, it is noteworthy that Wodehouse (1936b) and Erdtman think the peculiar polyporate pollen of Alismataceae might be derived from that of Ranunculaceae, although *Butomus* has monocolpate grains. Moseley sought to derive the acolpate, triporate pollen of *Casuarina* from a basically tricolpate condition in Hamamelidaceae; Erdtman tends to relate most of "the Amentiferae" on pollen structure.

Wodehouse contends that the various forms of pollen grain of angiosperms "have all been derived from each other by evolutionary processes" (1936a, p. 67). He quotes Fischer to the effect that the general trend has been toward a simultaneous strengthening of the outer spore wall, and the formation of prearranged exits for the pollen tube (1935). Adaptation to wind pollination leads to a progressive thinning and smoothing of the exine, until all anemophilous grains tend to resemble each other, irrespective of origin (Wodehouse, 1931, 1936a). Entomophily, on the other hand, frequently leads to an accumulation of oil in, and the marked adornment of, the outer spore wall, as especially well shown in Compositae (Wodehouse, 1931, 1935, 1936a). A suggestion that a ratio exists between size of pollen and length of style, indicating a phylogenetic trend toward decrease in spore size, has been offered by Covas and Schnack (1945). In his new book, Erdtman confines himself to "an interpretation of the deflection of the 'palynological compass needle' " (1953, p. 27), but his suggestions of presence or absence of affinity between many families makes fascinating study. With the probable exception of the significant distribution of monocolpate pollen and the specialized nature of that in "the Amentiferae," Erdtman's restraint seems to be entirely appropriate and to set the limits beyond which, as yet, we are scarcely prepared to go.

D. *Significance of embryological characters:* The foregoing extremely sketchy discussion of the embryological features of angiosperms gives point to the qualification of Maheshwari that "the embryologist would however be glad to admit that he lays no claim to erect a phylogenetic scheme of his own" (1945, p. 32). We can perhaps agree with Just:

> Embryological data need not be accorded more recognition than other taxonomically valuable characters. They do, however, deserve their rightful place among the others, a position they have not yet attained in the eyes of all botanists (1946, pp. 354–355).

If currently available information on the ovule and the gametophytes does not permit the erection of unique phylogenies, it does provide a whole galaxy of new characters. Many of those of possible taxonomic utility have been summarized by Netolitzky, Tischler, Schnarf, Wodehouse, Just, Maheshwari, and Erdtman. Of particular relevancy is the advocacy by Schnarf, Maheshwari, and Just of embryological diagrams and formulae, so that as many features as possible may be compared in determining relationship.

As we have observed to be the case with other anatomical characters, the results are frequently negative. The differences between two taxa may be so manifold that it seems unlikely that they bear any close relationship to each other

Thus, embryological characters are stated to demand exclusion of Lennoaceae from Ericales (Copeland, 1935a) and of *Polypremum* from Rubiaceae (Moore, 1948). They may point to possible affinities which need, however, to be checked by evidence of other kinds, as the relationship of *Adoxa* to *Sambucus* (Fagerlind, 1944), of Empetraceae to Ericales (Samuelsson, 1913), and of Podostemonaceae to Crassulaceae (Mauritzon, 1933). Such characters can be especially helpful when thrown into the scales to decide between supposedly conflicting relationships, as Cactaceae to Aizoaceae and Portulaceae rather than to Passifloraceae or Loasaceae (Neumann, 1935; Mauritzon, 1934), and Compositae to Calyceraceae and Dipsacaceae rather than to Cucurbitaceae or Campanulaceae (Poddubnaja-Arnoldi, 1931; Schnarf, 1931, 1933). They can perhaps be of greatest service in testing the naturalness of taxonomic groups and in revising internal arrangements. Venkateswarlu (1952) verifies the distinctness as a family of Lecythidaceae, and Palser (1951, 1952) establishes the basic agreement between data from the megagametophyte and from floral anatomy in Andromedeae of Ericaceae. Within Plumbaginaceae, Baker (1948) found that pollen morphology, embryo-sac type, and apparently chromosome numbers could be correlated to distinguish the tribes Staticeae and Plumbaginae. On the basis of embryological features, and making use as well of interesting cytological peculiarities (McKelvey and Sax, 1933; Whitaker, 1934; Granick, 1944), Wunderlich (1950) has found that the Agavaceae of Hutchinson—although the basic *Yucca-Agave* relationship is valid—contain diverse elements, perhaps too various to be retained within the same family. Because more embryological data are known for them than for any other family, Cave's (1948, 1953) application of Maheshwari's embryological criteria to the delimitation of subfamilies, tribes, and genera of Liliaceae suggests how rewarding this approach can be at its best. It also underlines, however, how far we still have to go in the systematic accumulation of information before we can hope for similarly profitable exploitation of embryological data in other groups.

Typological series, based on the initial stages of embryological development, have been proposed by several authors (Johansen, 1950) but, because they have rarely been utilized taxonomically, these will not be discussed here.

Fruit and Seed

Fruits, especially, and seeds have long provided taxonomists with important systematic characters, but there have been few serious attempts to work out a consistent evolutionary scheme for either category of structure. Obviously, the nature of the fruit depends primarily upon the constitution of the gynoecium of the flower, that of the seed upon the ovule. Several authors have stressed the idea that seed disperal is a critical phase in the life cycle of the plant, and one during which the forces of natural selection have a maximum opportunity to exert their effect (Corner, 1949; Stebbins, 1951). Stebbins has stressed the important consideration that selection operates on *combinations* of characters, so that what types (primitive or advanced) of vegetative and reproductive structures will be found in successful association depends upon the habitat in which the plant lives, and the various agents of pollination and seed dissemination available to it. Bews and Corner regarded seeds with short viability and little or no capacity for dormancy in noncapsular (Bews) or follicular or capsular (Corner) fruits to be primitive in tropical and subtropical environments. Polyspermous fruits were believed by Robertson and Gunderson to be related to animal dissemination, while those with only one or a few ovules bespoke anemophily; Neumayer and Janchen, of course, believed the latter condition to be primitive. Salisbury (1942) found a correlation of the weight of fruit or seed with the degree of shading to which the seedling would normally be subjected. He found also that, at least in the British flora, the greatest seed output characterizes opportunistic ruderal plants, the lowest to be associated with shade-loving herbs. A relationship between the possession of fleshy fruits and a woody or herbaceous-climbing habit, and between dry fruits and herbaceous-terrestrial habit was postulated by Sinnott and Bailey (1915a); this was questioned by Bancroft (1930). Porsch (1931) called attention to scarlet as the color most likely to attract animals, an idea which Corner exploited. Both Odell and Elias (1946) have emphasized the importance of fossil fruits and seeds as more decisive than leaves and more abundant than preserved flowers.

A. *Fruits:* Baumann (1946) has recently stressed the development of a dry schizocarpous fruit from a baccate one in *Myodocarpus* to explain the derivation of Umbelliferae from Araliaceae. Although the generally accepted close affinity of the two families has recently been abundantly confirmed on anatomical evidence (Rodríguez, 1953), it is difficult for me to believe that an implied derivation of *Trachymene* from *Myodocarpus* can explain the origin of the subfamilies Apioideae and Saniculoideae of Umbelliferae. An interesting example of the diversification of a single fruit-type, presumably under drastic environmental selection, is given by Zohary's (1950) study of the fruiting head of Compositae. In Ranunculaceae, Rassner attempted to show that the follicle is basic to all other fruit types; the reduction of follicles to achenes was well established by Chute (1930) in both Ranunculaceae and Rosaceae, on the basis of vasculation. Stressing its loculicidally dehiscent capsular or baccate fruit, Edlin transferred Hibisceae bodily from Malvaceae to Bombacaceae, a transfer opposed by C. V. Rao (1952) on grounds of seed anatomy, cytology, and pollen morphology. Both Edlin and Rao believed the multilocular schizocarpous fruits of *Malva* section Malopeae to be derived by "chorisis." A "splash-cup" mechanism of seed dispersal, favoring the development of shallow, erect, open capsules in at least one evolutionary line of Saxifragaceae, is postulated by Savile (1953).

In an ingenious *tour de force* (perhaps parodying exclusively floral phylogenies?), Corner assumes as primitive for all modern flowering plants "the red, fleshy, and often spiny follicle or capsule, with large black seeds covered by a red or yellow aril and hanging from the edges of the fruit-valves" (1949, p. 376). From this initial supposition he concludes (p. 396):

> The immediate ancestors of modern flowering plants must have been sparingly and sympodially branched, soft-wooded, tropical trees of low or medium height, with massive twigs bearing spirally arranged compound leaves without distinct internodes, and reproduced by large arillate seeds borne on massive red follicles, succeeding terminal flowers or inflorescences. The more remote ancestors appear to have been monocarpic and monocaulous, with the Cycad-habit.

He points out that "the Amentiferae" represent an unnatural mixture of megaspermous and microspermous plants, and adds that microspermous herbs could not have given rise to megaspermous trees. Like all phyletic schemes based on a single feature, this Durian theory is more entertaining than convincing.

The standard textbook classifications of fruits and seeds are obviously artificial, teleological, and thoroughly unsatisfactory. Two modern students, Winkler and Guşuleac, have attempted to subordinate the fascinating biological aspects of fruit- and seed-dispersal, and to relate fruit classification squarely to the structure of the floral gynoecium. The fruit, it appears, is almost as difficult to define as is the flower. Knoll (1939), following Gaertner and Goebel, designated as fruit all parts of the flower remaining at the time of seed ripening; Winkler (1939, 1940) and Guşuleac (1938a, 1938b), on the example of Pax, restricted the fruit to that structure which arises from the gynoecium as a consequence of fertilization or parthenocarpy. Accepting the foliar interpretation of the carpel, both Winkler and Guşuleac regarded as primitive those fruits derived from apocarpous gynoecia, those from syncarpous (paracarpous, coenocarpous) gynoecia as advanced. The classification proposed by Winkler (1939, 1940) has two main divisions, the apocarpous *Sammelfrucht* and the syncarpous *Einheitsfrucht*. These two major divisions are then each subdivided on the basis of superior versus inferior ovary, and the resultant four subdivisions on the criterion of dry versus soft-fleshy texture. Guşuleac (1938a, 1938b) proposed four principal categories: *Apokarp, Eusynkarp,* and *Apokarpoid* (syncarpous but separating into carpellary units), each representing the entire gynoecium of a single flower, and *Zönanthokarp,* an artificial grouping of all "false fruits" derived from the gynoecia of two or more flowers. The apocarpous group is bisected according to whether the gynoecium consists of a single, or of two or more carpels; the syncarpous group according to whether the gynoecium is pluriloeular or unilocular; and the apocarpoid group according to whether the disintegration of the mature fruit yields pieces equivalent to whole or to only partial carpellary units. Each of these six subdivisions is then redivided into a capsule-, a nut-, and berry-, and a drupe-series. The three prime categories of this system, as thus aligned, are supposed to represent a phylogenetic series, but in a second article the same year, the *Eusynkarp* and the *Apokarpoid* groups were transposed. Winkler stressed the follicular carpel as the basic unit of all angiospermous gynoecia and attempted to show that the elements of a septicidally dehiscent capsule are each fully equivalent with such a free carpel (1936b, 1939, 1940, 1941; Juhnke and Winkler, 1938). To Winkler, Guşuleac's fruit-series should then be read in accordance with the advancing grade of syncarpy, viz.: (1) carpels free—apocarpous, choricarpellous; (2) carpels weakly united and separating in fruit—apocarpoid, dyssencarpellous; (3) carpels strongly united and not separating into units corresponding with carpels—eusyncarpous, syncarpellous. Both authors, it is to be noted, accepted the view that analogous dehiscent or indehiscent, dry or fleshy, and one- or several-seeded fruit types can arise anywhere along this sequence, presumably as a result of the selection pressure of biological demands. The loculicidally opening capsule, also, is regarded as a biological rather than a basic, phylogenetic type. The evolutionary validity of such classifications as the two just described is attested by the fact that members of the same taxonomic groups are found to be characterized by the same or closely related fruit types. This situation is strikingly different from that which obtains when the biological fruit arrangements of the nineteenth century are applied to related taxa.

B. *Seeds:* As pointed out by Netolitzky, we actually know so little about seeds in the angiosperms as a whole that it is difficult to use them systematically or to distinguish between structural features which are sufficiently stable to be taxonomically reliable and those which are susceptible to ecological modification. A correlation exists, according to Salisbury (1942), between the amount of reserve food in the seed and the position the plant normally occupies in plant succession. In some families and genera, seeds have been studied with sufficient thoroughness to permit the establishment of a basic or ideal "type" for the group, making possible comparisons with those of other groups. Stressing the fundamental importance in classification of seed structure, Corner (1951) finds that seed morphology strengthens the unity of Leguminosae, and separates the family clearly from Rosaceae. Kratzer (1918) demonstrated the application of comparisons of seed development to indicate that Cucurbitaceae could not be related to Campanulaceae, Loasaceae, Aristolochiaceae, Begoniaceae, or Ebenaceae; Aristolochiaceae and Loasaceae could not be related to Caricaceae and Passifloraceae; and Caricaceae could not be related to Euphorbiaceae. Findings from seed characters, he warned, are largely of negative value and cannot be used in disregard of evidence from other features of the plant. Reeves and Hutchinson (1947) have successfully employed seed characters taxonomically in Malvaceae, Riek-Haussermann (1944) used them within the genus *Veronica,* and Buxbaum attempted to relate Cactaceae with Caryophyllales by mutual possession of a type of arillate seed. Murley's (1951) painstaking investigation of seed structure in Cruciferae, beautifully illustrated, exemplifies the kind of information required to permit more general and productive use of seed characters in classification.

Well-established phylogenetic trends are few and shaky in this area, as should be expected from the dearth of extensive comparative (systematic) data. Arillate seeds were regarded by Sporne as primitive, because of a positive correlation with other characters believed to be primitive, and Corner assigned them a major role in his hypothetical primitive angiosperm. However, Netolitzky thought all such features as arils and wings to be specializations. The last author stressed that retention by seeds of indehiscent fruits of a well-developed testa is an indication of an ancestral condition, since in such cases the pericarp tends to take over the protective function of the seed coats. Thus, the thinning of seed coats seems to be a general evolutionary advance; the reduction of nutritive tissue and of the embryo, or the filling of the latter with reserve foods, are usually regarded as advances, also. Nagaraj (1952) cities the lack of endosperm in the seeds of Salicaceae as an argument for an advanced rather than a primitive position for this family.

The only attempt to develop a comprehensive phylogenetic classification of seeds of which I am aware is that of Martin. The result of an examination of the seeds of more than twelve hundred genera, the scheme places primary emphasis on the shape, size, and position of the embryo. Some confusion was caused by the fact that the author reduced his major divisions from three to two in a terminal footnote of the same paper, with the remark: "The resulting two divisions, Peripheral and Axile, seem to represent well the two main lines of seed evolution" (1946, p. 529). There appears to be some correlation between a parietal (peripheral) embryo and starchy endosperm, and a central (axile) embryo with relatively nonstarchy endosperm, if any. Subordinate to the two divisions are twelve "types." Martin suggests a few trends which he regards as evolutionary, beginning with primitive medium-sized or large seeds containing relatively small embryos and manifesting early dormancy. Two trends in size are evident, the one leading to quantity production of minute and delicate seeds (microspermy), the other to the formation of a few large, well-stocked, relatively large-embryoed ones (megaspermy). A study of the "family tree" is very instructive, although the author warns that it is not meant to represent a new classification of families for general purposes, or to supersede data from other lines of evidence. There appears, for instance, to be a close correlation in seed type between Nymphaeaceae and Saururaceae with certain monocotyledons; Cyperaceae and Gramineae manifest important differences; seeds with a curved peripheral embryo—Caryophyllales, Cactaceae, Frankeniaceae—are regarded as an evolutionary blind alley. Although such an angiospermous "seed phylogeny" is obviously premature, it seems to indicate that there do exist characters and trends which might be employed not only for taxonomic but also for phylogenetic objectives.

Comparative Biochemistry

The idea that comparative biochemistry, like comparative morphology, anatomy, and embryology, can furnish significant evidence for relationship and classification is attractive and probably theoretically sound. Indirectly, such chemical features as the presence of latex, resins, volatile oils, and the possession of different kinds of endosperm have long been employed in the recognition of members of certain families and genera, and even as suggesting affinity between families.

The distribution of anthocyanins in flowers, it has been suggested, possibly has "some phylogenetic significance, although there are obvious limits to the conclusions which may be drawn" (Lawrence *et al.*, 1939, p. 173). The possession of nitrogenous anthocyanins affords an additional agreement between Cactaceae and families of Caryophyllales (Gibbs, 1945). The occurrence of fats and fatty acids in plants "runs on the whole remarkably parallel with the groups into which morphologists have placed them" (Hilditch, 1940, p. 14). However, "the biogenesis in plants of fats from carbohydrates remains indeed an uncharted and mysterious field" (Hilditch, 1952, p. 182). Potentially, the comparative biochemistry of essential oils, as applied by Baker and Smith (1920) to *Eucalyptus*, holds considerable promise (McNair, 1942). Plant alkaloids which are specific in their occurrence may also be of classificatory value since, according to Weevers, "a close relation exists between the nature of the chemical products and the taxonomical position of the species, genus or family which produce them" (1943, p. 421; McNair, 1935a; Weevers, 1933).

In his exhaustive monograph of starches and their reaction-curves Reichert, although acknowledging "the very limited range and preliminary nature" of his research, emphasized the worth "of the molecular characters of products which are passive, nonstructural constituents of the plant" (1913, p. 340). He also gave examples to suggest the desirability, on this basis, of subdividing the families

Liliaceae and Iridaceae. The chlorination of lignin (Maüle reaction) has been used as a specific test for angiospermous wood. It is of interest that all three genera of Gnetales give a similar reaction (McLean and Evans, 1934; Gertz, 1943), but the phylogenetic implications of this striking fact are weakened by the discovery that one out of seventeen species of *Podocarpus* treated gave a weak but positive reaction, also (Crocker, 1933).

McNair, in a series of papers (1934, 1935a, 1935b, 1942, 1945a, 1945b), has attempted to establish correlations of chemical changes with the degree of evolutionary advancement of the plants in which the chemical substances occur. Thus he states that with phylogenetic specialization: (1) unsaturated oils tend to increase at the expense of saturated ones; (2) the size of molecules tends to increase, the molecular weight of alkaloids increases, and the specific gravity of volatile oils mounts while their index of refraction declines; (3) the number of fatty acids in fruit and seed fats tends to increase; (4) the heat of combustion of fatty acids and alcohols increases; (5) the iodine values of glycerides increases; and (6) the orientation of hydrocarbons tends to shift from dextro- to laevulo-rotary. On the basis of these postulates, he concludes that apocarpy, choripetaly, and woody habit are more primitive than syncarpy, sympetaly, and herbaceous habit, that Magnoliaceae are more primitive than Ranunculaceae or Berberidaceae, that oligocarpy is at least as archaic as polycarpy, and that monocotyledons are older than dicotyledons.

The most spectacular results and the hottest controversy have come from the serological testing of protein specificity as providing clues to affinity, and culminating in the famous "Königsberger Stammbaum" (Mez and Ziegenspeck, 1926). The literature, especially German, of the 1920's and 1930's is replete with criticism, counter-criticism, and polemic between adherents of the various "schools" of serology (Worseck, 1922; Mez and Ziegenspeck; Gilg and Schürhoff, 1926; Wermund, 1928; Moritz, 1929, 1934; Roederer, 1930; Ruff, 1931; Krohn, 1935; Mez, 1936). The degree of positiveness on both sides is striking and appears to conform very poorly with scientific objectivity. The following quotation may be regarded as not wholly atypical (Krohn, 1935, pp. 370–371).

> Accordingly all conclusions derived from serological species-reactions must be taken as conclusive for the relationship of the whole families. . . . Morphology and serology are never in contradiction, in the contrary they are furnishing reciprocal corroborative results. . . . My control-tests are supporting the present classification of the Königsberg-Genealogical tree, in opposition to the publications of the Berlin School.

Chester (1937) has reviewed the subject of the serological approach to plant relationship with sympathy, indicated his faith in its theoretical soundness, and suggested that differences in method might account for the conflicting results obtained by different workers. He also stressed the fact that plant antigens are the consequence of a whole mosaic of individual reactions and should, therefore, afford a superior measurement of relationship. By the comparison of isoelectric points of latex proteins, Moyer (1934a, 1934b, 1936) has attempted to determine species affinities and to correlate the position of isoelectric points with chromosome number in *Euphorbia* and *Asclepias*.

Redfield supplied a needed caution against the too exuberant application of chemical characteristics to phylogeny, in the following words (1936, p. 122):

> Much of physiology is by nature analogous—being the fortuitous combination of

factors to serve a complex end. The morphological factors are the province of comparative anatomy; the chemical factors deserve treatment by a similar discipline. Before they can aid us in understanding the evolutionary problem, we must develop criteria for judging their true homologies. This will come as we learn more of the origins of the substances we find in particular organisms and understand something of the mechanisms underlying their multiplication and variation. When it comes our studies will be on a new footing.

Primitive Habit of Angiosperms

The groups of dicotyledonous angiosperms postulated as most primitive in the current phylogenetic classifications, with one exception, are indicated as being perennial, woody, and arborescent. The system of Hutchinson visualizes separate woody and herbaceous lines of dicots. The large measure of agreement on the priority of woody habit is based on: (1) the prevalence of woody habit in gymnosperms; (2) its correlation with anatomical and floral characters regarded as primitive and, conversely, the association of advanced anatomical and floral characters with herbaceous habit; (3) the predominance of woody plants in moist tropical and subtropical areas, habitats which are widely believed to be the modern equivalents of the climatic conditions widespread at the period of angiosperm inception; (4) the revelation of the peristence of cambium in seedling and herbaceous stems; (5) the supposed correlation between fleshy fruits and woody habit; (6) the evolution in vascular crytogams from protostele to siphonostele to eustele; and (7) the lack of undoubted fossil herbaceous angiosperms in older geological strata. Bews stated his conviction that "the earlier fossil Angiosperms were closely similar to the types now occurring in moist and subtropical areas" (1927, p. 20), and visualized this ecological type as having given rise both to the trees and shrubs of arid and temperate regions and the lianes, epiphytes, and herbs developing within forest understories, openings, and margins, and spreading outward. Andreanszky (1950, 1952) entertains similar views, but believes that such aquatics as Nymphaeaceae were formed very early. Davy suggested that the suffruticose habit forms "an intermediate stage in the evolution of an herbaceous from an arborescent type" (1922, p. 219). Sinnott and Bailey stipulated that "the herbaceous vegetation of today should be regarded as of comparatively recent development" (1914, p. 595; 1915a, 1915b; Eames, 1911; Sinnott, 1916; Jeffrey and Torrey, 1921).

The chief recent opponent of the primitiveness of arborescent habit has been Arber. She suggested that the wide distribution of herbs argues for their antiquity, that the separate vascular bundles of dicot herbs could not have been attained by the progressive dissection of a continuous woody cylinder, and that any correlation of primitive features with arborescent habit was due to the "evolutionary lag" imposed by the longer life-span of woody as opposed to herbaceous plants.

> The frequency of the tree habit in Angiosperms is held to point to the extreme antiquity of the flowering plant stock, which has allowed time for many lineages to reach a phase of senility; for trees show two characters which are indicative of old age in animal races—growth to a relatively large size, and the accumulation of non-living material in the body (Arber, 1928, p. 83).

She pointed to Agavaceae, *Clematis,* and *Berberis* as examples of the origin of woody from herbaceous types. Schellenberg and Cockerell (1935) state that if early angiosperms were herbaceous rather than woody, their absence from the fossil record would be explained. Some cytological support for Arber's views has been proffered by the work of Müntzing (1936) on polyploids, Senn (1938) on Leguminosae, Baldwin (1940) on Crassulaceae, Gregory (1941) on Ranunculaceae, and Perry (1943) on Euphorbiaceae. These cytologists have noted a correlation of higher chomosome numbers with woody or perennial habit, and of lower ones with herbaceousness or annual duration of growth. Bancroft (1930), who reviewed this problem in some detail, concluded that there was no reason to suppose that *both* trees and herbs might not have been represented in the stock whence angiosperms arose and that, therefore, it was not necessary that either condition be considered immediately primitive for the group. The existence of a primitive herbaceous flora, giving rise to herbaceous Gnetales and angiosperms, and only later in its history to a few woody plants, was visualized by Chamberlain (1920). Wettstein suggested that modern flowering plants arose from a group of Mesozoic "Protangiosperms" which contained both woody and herbaceous dicotyledons and monocotyledons. Metcalfe (1946) pointed to the lack of satisfactory anatomical criteria with regard to the herbaceous habit, and mentioned the importance of finding a method for comparing closely related trees and herbs if an over-all phylogeny of the dicots is to be developed.

Bailey (1949, 1953) emphasizes that the "tracheary phylogenies" mentioned above preclude the derivation of structurally primitive arboreal dicotyledons or of monocotyledons from herbaceous dicotyledons. He remarks especially the absence of any "structurally primitive, vesselless herbaceous dicotyledons. A vast majority of the herbs exhibit highly evolved vessels of much advanced form" (1953, p. 7). It is perhaps significant that those who have regarded herbs as ancestral to woody plants have been chiefly concerned with the study of monocotyledons. The authors citing the higher chromosome numbers of woody plants and perennials in comparison with annual herbs have tended to overlook the correlation of the perennial habit with polyploidy (Stebbins, 1938; Britton, 1951), a phenomenon which could explain some of their statistical data. Atchison (1947a, 1947b), Stebbins, and Darlington (1952) have all remarked the stability of chromosome number in woody plants as an evidence of the ancientness of the type. Sporne found a correlation between the fossil dicots of the Eocene London clays and some 47 families identified in pre-Pleistocene deposits, and concluded: "The 'primitive flowering plant' was, apparently, a tree" (1948, p. 46) and "the arborescent habit is in fact primitive and the herbaceous advanced" (1949, p. 271). Brown, on the basis of the seriation of types of floral nectaries, believed he had found evidence for the derivation of herbaceous from woody forms, as did Corner in the greater capability of trees to sustain massive fruits. Emphasizing the mechanics of herbaceous stems, Smith (1950) believes that herbs may have arisen both by the aggregation of rays to break the xylem clinder into separate bundles, and by the thinning of the vascular cylinder and reduction of cambial activity. Dormer, working with Leguminosae, concludes that herbaceous forms could have arisen only after a closed, tangentially continuous vascular system was produced, so that the continuous cylinder of secondary tissues is no longer necessary. Boureau thinks that seedling anatomy indicates "le type arbre, dans un phylum donné comme étant plus primitif que le type herbacé" (1952, p. 179). Finally, McNair finds data from the distribution of fats and other chemical substances to convince him that herbs may have been derived from trees.

The present weight of evidence suggests to me that, in general, modern herbaceous types may have been derived from more primitive woody ones, and that the opposite derivation appears to be highly unlikely. This does not preclude the likelihood that some apparently "woody" members of predominantly herbaceous families may not have arisen secondarily (Cotton, 1944). Neither does it rule out the possibility that herbaceous primitive angiosperms existed, but a demonstration of both their existence and of their archaic character is still awaited.

Status of "the Amentiferae"

A major point at issue between existing schemes of classification hinges on the interpretation of the woody, catkin-bearing, largely anemophilous dicotyledons producing predominantly unisexual flowers with no or poorly developed perianth, and often exhibiting "breech-fertilization," or chalazogamy. The arrangements of Engler and Wettstein, emphasizing the similarity of these so-called "Amentiferae" to living Gnetales and Coniferales in inflorescence, embryology, and mode of pollination, treated them as having a direct origin from gymnospermous types. Foreswearing a strictly phylogenetic arrangement, Rendle (1925) grouped his orders by grade of differentiation in floral structure, and commenced his system with six orders of "Amentiferae." Bessey, Hallier, Arber and Parkin, Parkin (1952), Hutchinson, Eames, Schaffner, Wieland, Mez, Wodehouse, Copeland, Lawrence (1952), and Puri, among others, construe this group of dicots as an artificial aggregation of highly specialized families, whose features of apparent simplicity owe largely to what Stebbins (1950, 1951) considers a general evolutionary trend toward reduction and fusion in angiosperm flowers, presumably as a consequence of the major shift in agency of pollination. A number of authors, encountering difficulty in deriving this group from bisexual forms or in deriving predominantly bisexual types, like Ranales, from unisexual ones, have suggested a biphyletic or polyphyletic origin for the angiosperms as a whole (Karsten, 1918; Sprague; Campbell, 1928; Davy, 1937; Gunderson, Fagerlind, Lam, Metcalfe and Chalk, Suessenguth and Merxmüller).

Engler seems to have included in "the Amentiferae"—although no such group-name is employed—the following eighteen families: Casuarinaceae, Saururaceae, Piperaceae, Hydrostachyruaceae, Saliceae, Garryaceae, Myricaceae, Balanopsidaceae, Leitneriaceae, Juglandaceae, Julianiaceae, Batidaceae, Betulaceae, Fagaceae, Ulmaceae, Rhoipteleaceae, Moraceae, and Urticaceae. Wettstein regarded Casuarinaceae, Garryaceae, Salicaceae, Batidaceae, Moraceae, Cannabinaceae, Ulmaceae, Urticaceae, and Piperaceae as groups evincing the same "morphological stage" as the remaining amentiferous families, but having no, or no clear, genetic connection with them. Rendle recognized an amentiferous grouping comprising Salicaceae, Garryaceae, Myricaceae, Juglandaceae, Julianiaceae, Betulaceae, Fagaceae, and Casuarinaceae; these he regarded as "isolated remnants of relatively ancient groups which have no descendants among the more highly developed orders of our present-day flora" (1925, p. 41). Hjelmqvist conceived of Casuarinaceae as near but not in "the Amentiferae," which he restricted to

Juglandaceae, Myricaceae, Balanopsidaceae, Leitneriaceae, Fagaceae, Betulaceae, Corylaceae, and Salicaceae, the Urticales, *Rhoiptelea*, and Proteales possibly being connected with them. A similar disposition is supported by Janchen (1950).

Thus, the questions whether "the Amentiferae" represent a natural group or an artificial one containing unrelated families and whether they are primitively simple, exhibiting direct connection with the gymnosperms, or their present features are derived from ancestral forms with more complex flowers may be tested in a relatively few families, as follows:

1. CASUARINACEAE. Casuarinaceae (Verticillatae) were placed at the very beginning of the angiosperms by Engler and by Wettstein; Rendle placed them as his sixth order. Schnarf and Hjelmqvist have regarded the family as truly primitive on the basis of embryological features presumably connecting them to gymnosperms. Lam places them together with the Gnetales in the "Protoangiospermae," but "without any phylogenetical meaning." Gaussen thinks they may stem directly from the Articulatae! Evidence derived from stem anatomy (Bailey and Sinnott, 1914; Tippo, 1938; Moseley), floral features (Moseley; Corner; Eames, 1951), and pollen (Moseley) seems to support the view that "the Casuarinaceae are a specialized family of the Angiosperms and are not a primitive group" (Moseley, 1948, p. 276), perhaps derived from Hamamelidaceae, as suggested by Tippo, Copeland, and Moseley.

2. FAGALES. George (1931) stressed the similarity in vegetative features between Gnetaceae and Fagaceae. The presence of aggregate rays, according to Hoar (1916), suggested that Betulaceae and Casuarinaceae should both be placed low in the phylogenetic scale. However, evidence from stem structure (Bailey and Sinnott, 1914; Hall, 1952), the inflorescence (Rickett; Langdon, 1947), and the flower (Berridge, 1914; Abbe, 1935, 1938; Wilson and Just; Porsch, 1950) provides more than a hint that this is a highly reduced group, with possible affinities to epigynous Rosales.

3. JUGLANDALES. Hagerup (1938) considered the structure of the gynoecium as indicating that Juglandaceae, together with Piperales and Caryophyllales, belong in the same evolutionary line with Gnetales and Coniferales, and Hemenway (1911) regarded the phloem of the family as relatively primitive. However, evidence from wood anatomy (Heimsch, 1938; Heimsch and Wetmore), the inflorescence (Manning, 1938, 1940, 1948; Rickett), and floral anatomy (Manning, Wilson and Just) appears to bear out the view that the primitive Juglandales were plants with a paniculate inflorescence, bisexual flowers with a prominent perianth, numerous stamens, several carpels, and possibly a capsular fruit. The modern members of the alliance exhibit a high degree of reduction. Withner (1941) considered *Rhoiptelea* to represent a relatively primitive member of this order. Convincing data have been gathered together by Withner, Heimsch (1942), Hjelmqvist, and Stern (1952) to show that Julianiaceae do not belong either in or near Juglandales, but possess affinities rather with Anacardiaceae.

4. SALICALES. Sporne, consistent with his contention that angiosperms had primitively unisexual flowers, regards the group as "quite primitive," and von Tuzson (1936) thought *Salix* one of the most archaic of dicots. However, evidence from the structure of the wood (Holden, 1912; Eames, 1951), the nature of the inflorescence (Fisher, 1928), floral anatomy (Fisher, Eames, Wilson and Just; Nagaraj, 1952), and embryology and cytology (Wilkinson, 1944; Nagaraj) appears to establish a strong inference that poplars and willows "though doubtless belonging to one of the more primitive lines of angiosperms, are far from primitive" (Eames, 1951, pp. 30–31). Even if the view is accepted that the order is a derived one, it is not clear what relationships it exhibits to other angiosperms: Bessey related it to Caryophyllales, Brown and Gunderson to Parietales or possibly Rhoedales.

5. URTICALES. Evidence for the advanced rather than primitive status of Urticales is based on the anatomy of the stem (Chalk, 1937; Tippo, 1938, 1940) and the flower (Bechtel, 1921; Eames, 1926; Eckardt). A relationship is suggested by Tippo, Copeland, and Moseley to Hamamelidaceae.

6. LEITNERIACEAE. Evidence that this monotypic family is a reduced member of either Rosales or Geraniales is found by Abbe and Earle (1940) in characters of the inflorescence and flower.

7. GARRYACEAE. Evidence that Garryaceae are not primitive but highly specialized and reduced has been adduced by Hallock on data from the inflorescence and flowers. She suggests that these plants are the "highest of the Umbelliflorae" (1930, p. 810), an affinity accepted also by Hjelmqvist and Sporne.

The lack of any fundamental unity among the groups which have been referred to "the Amentiferae," the occurrence of such presumably advanced characters as syncarpy and epigyny, the ample evidence of extensive reduction in inflorescence and flowers, and the absence of derived herbaceous forms, appear to me to destroy completely the notion that this is a primitive group marking the transition between gymnosperms and angiosperms. Allen (1940), Lewis (1942), Whitehouse (1950), and Darlington (1939, 1952) present genetic evidence to show that the derivation of unisexual flowers from bisexual ones is highly probable, the converse essentially impossible, an argument which gives added importance to the widespread occurrence of abortive male or female structures in the unisexual flowers of "the Amentiferae." The parallel between the inflorescence and flowers of the group and the reductions apparent in those of such other angiosperms as *Acer* (Hall, 1951), *Platanus* (Boothroyd, 1930), Plantaginaceae, Ambrosieae, and Cyperaceae (Blaser), provides a strong intimation of the factors promoting structural degeneration. Similarities with living gymnosperms, including embryological ones (Maheshwari, Battaglia), are apparently analogous rather than homologous and many of them are very superficial. The vessel studies of Thompson (1918, 1923)—although attacked by Bliss (1921) and MacDuffie (1921)—have apparently been confirmed, and lead to Bailey's conclusion (1949, pp. 67–68):

> Such fundamentally significant anatomical differences form an insuperable barrier to a derivation of the angiosperms from the Coniferales or the Gnetales. Thus, the presence of vessels in both the Gnetales and the angiosperms, which has so frequently been cited as evidence of relationship, actually negates such relationship. There are similarities between the end products of tracheary specializations in *Gnetum* and certain of the dicotyledons, but they have arisen by entirely different developmental changes.

The supposed paleobotanical proof of the comparative antiquity of catkin-bearing angiosperms is inconclusive. As Axelrod remarks (1952, p. 29):

> The fossil record does not demonstrate whether the primitive flower was generally of a magnolian type . . . or whether the simple type of the Amentiferae (oak, willow, alder) comes nearer to the proangiosperms.

In short there is no basis for the supposition that there exists a natural group, "the Amentiferae," and the systems of Engler, Wettstein, and Rendle are unnatural in so far as the basic status accorded such an artificial group is concerned.

Origin and Relationships of Monocotyledons

A great deal of phylogenetic discussion has centered about the monocotyledons and their position in "the System." Some of the principal points at issue have been the following:

1. Is there real affinity between monocotyledons and dicotyledons, or do they

represent completely independent phyla which exhibit striking parallelisms and convergences?

2. Do the monocots or the dicots—the existence of an affinity being granted—represent the more primitive group, and monocotyly or dicotyly the ancestral condition?

3. Whatever their origin, are the monocotyledons a natural group or an artificial aggregation?

4. If they did have a single source, from what group were the monocots derived and under what conditions?

5. What living monocotyledons retain the greatest array of primitive features?

So great is the majority of those who have recognized a genetic relationship between monocots and dicots that we may properly note here primarily a few dissenting opinions. Lindinger (1910), stressing the loss of the primary root with the substitution of an adventitious system and the absence of vessels in the secondary xylem, concluded that monocotyledons have had a quite discrete origin. In the belief that flowering plants arose from several or many Mesozoic "Protangiosperms," some dicotylous, some monocotylous, separate origins for at least some groups of the latter have been proposed by several authors (Engler; Campbell, 1930b; Pulle, 1938; Schaffner). A separate descent from different members of the Bennettitales was urged by Calestani and Wodehouse (1936a); the latter even thought Nymphaeaceae might represent an independent line from the same source. Von Tuszon (1936) preferred separate but similar origins from Gnetales or Gnetales-like ancestors. A derivation of monocotyledons from Lycopodiinae and of dicotyledons from other vascular crytogams was proposed by Appl (1937, 1937–1938), who has advanced several remarkable but quite unsubstantiated speculations; Conzatti (1942) saw in *Isoëtes* a possible forerunner of Gramineae. Bertrand (1947b) would trace both groups—like all other major lines in tracheophytes—independently from unicellular green algae. In accordance with his stress on the importance of "stachyspory" versus "phyllospory," Lam regarded these conditions as outweighing the distinction between monocotyly and dicotyly; Pandanaceae, at least, he regarded as "stachysporous," the great bulk of monocotyledons as "phyllosporous." Liehr (1916) resorted to cytological investigation to settle the question of affinity between the great angiosperm classes, but was unable to reach any firm decision, perhaps because he confined his observations to three species from each of the two groups. The contrary view, that monocots and dicots actually differ very little from each other, has been expressed repeatedly (Bessey, Sargant, Arber and Parkin; Worsdell, 1908; Coulter and Land, 1914; Coulter, 1915; Parkin, Zinke, 1924; Glück, 1925; Campbell, Schnarf, Maheshwari; Metcalfe, 1946; Johansen). Indeed, Suessenguth (1921) went so far as to suggest that monocots are in reality only a conventional group "like the Sympetalae," and that several lines stemming from dicots may have reached a "monocotyledonous stage."

In the nineteenth century, monocotyledons usually preceded dicotyledons in the sequence of orders, but the pendulum has now swung far in the opposite direction. Of those few who have more recently reaffirmed the greater relative antiquity of monocots, Lindinger, Schaffner, Conzatti, and Corner have emphasized the retention of a cycad-like habit by woody monocotyledons. Schellenberg thought that lack of secondary growth, tristichous foliage, and trimerous flowers are primitive features. The idea that the monocotyledons, because many of their orders are sharply distinctive, must have had greater time to allow for more extensive decimation, was advanced by von Tuzson. McNair concluded that evidence from the comparative biochemistry of seed fats and other organic compounds indicates that monocots are both simpler chemically than dicots and older in terms of phylogeny. Worsdell was led to his preference for the monocots as the older group by adherence to the Phyton theory, and Domin (1931) by his Phyllome theory. The seniority of dicotyledons over monocotyledons, on the other hand, has been accepted on various kinds of evidence by Henslow (1893, 1911), Sargant (1902, 1903, 1904, 1905, 1908), Hallier, K. Fritsch (1905, 1932), Hill (1906), Arber and Parkin, Lignier (1908), Lotsy (1911), Bessey (1915), Chamberlain, Suessenguth, Parkin, Sprague, Ankermann, Bews, Hutchinson, Zimmermann, Cuénod (1932), Ponzo (1932), Worseck, Copeland (1940), Werth, and Gaussen.

To the earlier workers, the problem of relationships of the two great classes of flowering plants was nearly identical with that of the number of their seed-leaves. Lyon (1905) and Worsdell (1908) considered the single seed-leaf of monocotyledons to be homologous, not with any foliar structure, but with the haustorial "foot" of bryophytes, and that the dicotylous condition resulted from bifurcation of an originally solitary, terminal cotyledon. Sargant found anatomical evidence to convince her that dicotyly was the original condition, because Liliaceous seedlings showed traces of bilateral symmetry. For those who regarded paired, foliaceous cotyledons as a primitive attribute, it was reasoned that the monocotylous condition might have arisen either by *syncotyly* (Sargant, 1903, 1904, 1905, 1908; Arber and Parkin, Suessenguth; Ponzo, 1929) or by *heterocotyly,* through simple suppression of one cotyledon (Henslow; Coulter, 1915; Boyd, 1930–1931; Winkler, 1931) or by conversion of one cotyledon into an haustorial organ (Sargant, 1902; Hill) or the first foliage leaf (Bugnon, 1931). Bancroft (1914) has pointed out that asymmetrical syncotyly normally occurs in dicot seedlings only if they come from exalbuminous seeds; thus, by analogy, Alismatales would have to be primitively unilaterally symmetrical, Liliales bilaterally symmetrical. These facts, he thought, would necessitate the conclusion that unilateral symmetry, and Alismatales, are primitive for monocots, or that bilateral symmetry, and Liliales, are primitive, or that monocotyledons are diphyletic. Engler insisted that monocotyly and dicotyly are of equal value unless both conditions occur together in closely related plants. Noting the sporadic appearance of pseudomonocotyly in distantly related families of dicotyledons, Suessenguth suggested that true monocotyly may have arisen repeatedly and polyphyletically. According to Maheshwari (1950, pp. 429–430):

> There are no essential differences between the monocotyledons and dicotyledons as regards the development and organization of the male and female gametophytes and the endosperm, and the process of fertilization is the same in both the subgroups. Further, the differences in the organization of the embryo are not fundamental, for there are some dicotyledons in which only one cotyledon develops fully and the other becomes arrested, and some monocotyledons in which both cotyledons develop equally.

Although monocots have probably been regarded by most workers as a monophyletic group once its origin had taken place, there has been no dearth of dissenting opinions. Thus, at least a diphyletic origin was supported by Hill, Lotsy, Campbell, and Lam, while a possibly multiple origin has been advocated by Suessenguth, Engler, Ponzo, Calestani, and Gaussen. The seeming necessity for more than a single origin is owing, as in dicotyledons, principally to reluctance to accept derivation of apetalous and petalous, anemophilous and entomophilous, woody and herbaceous plants from each other.

The selection of an ancestral group largely determines, of course, which representatives of living monocotyledons are to be regarded as retaining the maximum number of primitive characters. These authors seeking a single source for the monocots have turned overwhelmingly to Ranales—living or extinct. Such features as plasticity and indefiniteness in number of floral parts, the regular or occasional occurrence of acyclic or hemicyclic arrangement, trimery, and a differentiated perianth, numerous stamens, successive pollen division and other embryological similarities, an apocarpous gynoecium, parietal placentation, the frequent lack of vascular cambium, and the preference for an hygrophytic way of life have all been given importance. Thus the supposedly closest ties have usually been found between Alismatales (Heliobieae, Butomales) and either Ranunculaceae (Salisbury, Wettstein, Wodehouse; Werth, 1941; Metcalfe) or Nymphacaceae and Ceratophyllaceae (Nitzsche, Worseck, Parkin, Ankermann, Troll, Eber, Andreanszky, Puri). Turning the tables, Schellenberg thought dicots might have been derived from monocots via Alismatales-Ranales. Worsdell suggested that both Ranunculaceae and Nymphaeaceae might have descended from monocotyledons; Earle (1938) found reasons for considering Nymphaeaceae, and both he and Mez and Ziegenspeck, Ceratophyllaceae as much monocots as dicots. Several authors have, however, disagreed with the postulation of affinity between Ranunculaceae and Alismataceae, contending that they are not so close as has been generally assumed (Hallier; Meyer, 1932; Troll, 1932; von Tuzson) and that neither family is by any means primitive (Corner). Cuénod (1932) believed monocotyledons to be derived monophyletically from dicotyledons, but was undecided whether the junction should be with Ranales or Caryophyllales. A possible connection between Ranales, in the vicinity of Berberidaceae, and Liliales (Liliiflorae) was postulated by Hallier. Sargant (1905), also, thought Liliales basic in the monocots, and Markgraf and Granick proposed Alismatales as a connecting link. Nicotra (1909–1910) regarded Alismatales as related with Nymphaeaceae but at the same time deemed Cyclanthaceae as being nearer the base of the monocotyledons.

Reluctant to derive woody plants from herbaceous forebears, Lindinger saw *Dracaena* as the *Urtypus* of monocots, a view apparently shared by Boureau. A similarity between "pachycaul" monocots and cycadophytes was mentioned by Corner, and a possible line of ascent from bisexual palms to Liliales was suggested on the basis of pollen by Wodehouse and on evidence from floral nectaries by Brown. Advocates of diphyletic, triphyletic, or polyphyletic derivation of the monocotyledons have tended to reconcile some of these differences, as well as to submit additional possibilities. Hill saw a derivation of aroids (Spadiciflorae) from Piperaceae, and of Liliaceae from Ranunculaceae, and Lotsy maintained a similar diphylesis. Descent of palms from Bennettitalean ancestors, and of Alismatales from Nymphaeceae, was offered by Calestani. Schaffner thought that *Yucca* and *Dracaena* are primitive in habit, Alismataceae and Palmaceae in floral organization. That the monocots had three independent original groups—Pandanales, Helobiae (Alismatales), and Glumiflorae—was indicated by Engler and favored by Campbell; Ponzo accepted these three and added Liliflorae (Liliales) as a fourth, all in turn to be regarded as offshoots of dicotyledons. Finally, Suessenguth thought he recognized such interclass connecting links as Cabombaceae–Butomaceae, Ranunculaceae–Alismataceae, Berberidaceae–Liliaceae, and Taccaceae–Aristolochiaceae.

Depending upon what kinds of plants were postulated as the source or sources of monocotyledons and the mechanism of cotyledonary change, it has frequently been suggested that monocots arose as an adaptation to aquatic or marshy habitats (Henslow, Bews, Andreanszky), or to a geophilous mode of life (Sargant, Hill, Ponzo), or to both (Arber and Parkin). Henslow felt that the aquatic environment had a "degenerating effect" upon structural features and pointed to the parallelism in loss of cambium and secondary growth, the scattering of vascular bundles, and parallel leaf-venation in hygrophilous dicots and monocots. Sinnott (1914) and Calestani emphasized that the development of sheathing leaf-bases might have led to a multiplication of both foliar and cauline traces, and hence to the production of multilacunar nodes and "endogenous" stem structure. Arber and Parkin suggested that in monocotyledons the evolutionary sequence might have been from herbaceous to woody types, reversing that assumed for dicotyledons. All of these explanations are, of course, highly speculative.

In her excellent monograph on monocotyledons, Arber expressed her well-known antipathy to the intrusion of phylogenetic speculation into the study of form pursued for its own sake. In her opinion (1925, p. 217),

> . . . the great groups of Monocotyledons have not achieved unlikeness by divergent modification, but they must have been of different types from the moment of their appearance. . . . We have no evidence from Palaeobotany for the former existence of synthetic types uniting any of the Monocotyledonous cohorts, and I am inclined to suppose that these great groups will ultimately be traced back to a very remote antiquity, without displaying a common origin.

She agrees that it would be logical to suppose an ultimate derivation of such stocks from a single, primeval "Urmonocotyledon," but believes that such an assumption is by no means proved and that we must, for the present, give up all hope of discovering either connecting links between the great groups of monocots or between monocots and dicots. In striking contrast with these rather pessimistic views is the brash comment of Ankermann that "today we may accept the system of monocotyles as perfectly worked out" (1927, p. 46)! Is there anything positive to be gained from this welter of hypothesis and counterhypothesis as to the origin and evolution of monocotyledons and their affinities with dicotyledons or other vascular plants? Or must we assume, on the basis of majority vote, that there is some kind of connection between florally unspecialized Ranunculaceae, Nymphaeaceae, and Alismataceae, and leave the matter at that point?

The recent extensive investigations by Cheadle on the vascular tissues of monocots, like those of Bailey on dicots, appear to offer us some hope, although Cheadle has been exceedingly chary of drawing phylogenetic conclusions. His work has revealed: (1) that in essential features the vessels in the primary xylem of monocots parallel the unidirectional trends established for those in the secondary xylem of dicots; (2) that a progressive series can be established for sieve tubes, depending upon the inclination of end walls and the nature of distribution of sieve plates; and (3) that the vascular bundles can be arranged in an ascending typological series depending upon the features of the xylem and phloem of which they are composed. Unlike the situation in dicots, in monocots vessels are believed to have originated in the late metaxylem of roots, and to have spread thence to the aerial portions of the plant. In general, these indicator series suggest that monocotyledonous plants which possess the largest amount of secondary tissue (produced by a thickening cambial ring) generally have relatively primitive sieve tubes and vessels in their roots. It is noted that typically bulbose or cormose plants usually possess vessels in their roots only. Highly specialized monocots, on the other hand, are those which have vessels with porous perforations and sieve tubes with transverse end walls distributed throughout the plant body. Among the groups which appear to be highly specialized because of the nature and distribution of their xylem and phloem elements are Gramineae, Cyperaceae, *Juncus, Cordyline,* palms, Pandanaceae, Typhaceae, Dioscoreaceae, and most Alismatales. Bailey has gone further than Cheadle in interpreting the classificatory significance of these studies (1953, p. 7).

> We now know that there has been an independent evolution of vessels in dicotyledons and monocotyledons, and if the angiosperms are monophyletic, that the two great groups of plants must have diverged before the acquisition of such structures in either group. . . . Obviously the structurally more primitive types of monocotyledons cannot be derived from such highly modified and specialized plants as the herbaceous Ranunculaceae or Piperaceae.

Bailey's and, I judge, Cheadle's concept of a fundamentally primitive monocotyledon would perhaps not be too strongly at variance with Lindinger's postulation of *Dracaena* as an *Urtypus.*

Although warned by both Arber and Bailey (1953) that any attempt to bridge the gap between monocotyledons and dicotyledons must be regarded as purely speculative at this time, it may be worthwhile if only to prevent the Ranunculaceae–Alismataceae or Nymphaeaceae–Alismataceae hypotheses from hardening into textbook dogma. It would seem that the similarities between dicots and monocots are too profound and too numerous to be dismissed as mere analogies, parallelisms, and convergences. The Ranales are unique among dicots in possessing members with the monocolpate type of pollen which characterizes most monocots and gymnosperms—the true character and significance of that in Alismatales appears to be debatable (Wodehouse, 1936b; Erdtman, 1953). The Ranales are unique among angiosperms in possessing primitively vesselless secondary xylem. The perianth-bearing flowers of some Ranales, with leaflike sporophylls of both sexes, may be regarded as "standard" also for most monocots—even Cyperaceae (Blaser, 1941), Gramineae; Aponogetonaceae, Potamogetonaceae, Najadaceae (Markgraf); Araceae (Arber), and Palmaceae (Bosch); whatever the true nature of the monocot perianth may be, all the same possibilities of derivation have been suggested also for the perianth of Ranales. Fries (1911) called attention to the occurrence in Annonaceae of an arrangement of prophylls which is characteristic of monocotyledons. The many structural parallels between herbaceous Ranales and Alismatales have already been mentioned, but it must be remembered that these herbaceous groups are highly specialized in vegetative if not in floral characters.

Thus, we are confronted by the paradox that, although similarities between certain Ranales and certain monocotyledons are legion, they must have diverged from a common ancestor before the development of vessels. My own suggestion would be that a common origin for monocots and dicots is more likely than wholly distinct origins, that the ancestral type might have been a woody, vesselless "Pro-Ranalian," and that the primitive monocot is perhaps best—but not very well—represented today by certain Liliales which have retained a capacity for relatively regular secondary growth. Some palms and Alismatales appear to retain a less modified floral structure (apocarpy), but they seem precluded by their other features from occupying a position anywhere in the huge evolutionary gap which this suggestion envisages. It should not be forgotten that the primitively vesselless dicots do not necessarily have floral structure apparently as primitive as that of certain herbaceous Ranunculaceae. That some groups of monocotyledons could have had a different origin from that here indicated does not seem to be completely ruled out but, as in the case of the possible existence of primitive herbs, the burden of proof is on the advocates of polyphylesis.

BIBLIOGRAPHY

ABBE, E. C.

1935. Studies in the phylogeny of the Betulaceae. I. Floral and inflorescence anatomy and morphology. Bot. Gaz., 97:1–67.

1938. Studies in the phylogeny of the Betulaceae. II. Extremes in the range of variation of floral and inflorescence morphology. Bot. Gaz., 99:431–469.

ABBE, E. C., and T. T. EARLE

1940. Inflorescence, floral anatomy and morphology of *Leitneria floridana*. Bull. Torrey Club, 67:173–193.

ALLEN, C. E.

1940. The genotypic basis of sex expression in angiosperms. Bot. Rev., 6:227–300.

AMES, O.

1937. Pollination of orchids through pseudocopulation. Bot. Mus. Leafl., 5:1–29.

1946. The evolution of the orchid flower. Amer. Orchid Soc. Bull., 14:355–360.

ANDREANSZKY, G.

1950. Die Rechtlinien der Pflanzenphylogenie. Ann. Biol. Univ. Budapest, 1^1:19–20.

1952. Ueber die Rolle der limnischen Lebensweise in der Phylogenie der Pflanzen. Acta Biol., 3:19–30.

ANKERMANN, F.

1927. Die Phylogenie der Monocotyledonen; Versuch einer Einteilung der monocotylen Pflanzenfamilien und ihre Stellung zueinander auf Grund der Morphologie. Bot. Archiv, 19:1–78.

APPL, J.

1937. Versuch einer Ableitung der Monocotyledonen von den Lycopodiaceae. (Privately printed.)

1937–1938. Die Filixabkömmlinge der Angiospermen. Repert. Sp. Nov., 42:153–156; 43:77–80.

1939. Der Ursprung der Karpelle. Biologe, 8:335–336.

Arber, Agnes

1925. Monocotyledons, a Morphological Study. xiv + 258 pp. Cambridge: Univ. Press.

1928. The tree habit in angiosperms: its origin and meaning. New Phytol., 27:69–84.

1933. Floral anatomy and its morphological interpretation. New Phytol., 32:231–242.

1937. The interpretation of the flower: a study of some aspects of morphological thought. Biol. Rev., 12:157–184.

Arber, E. A. N., and J. Parkin

1907. On the origin of the angiosperms. Journ. Linn. Soc., 38:29–80.

1908. Studies on the evolution of the angiosperms; the relationship of the angiosperms to the Gnetales. Ann. Bot., 22:489–515.

Atchison, Earlene

1947a. Chromosome numbers in the Myrtaceae. Amer. Journ. Bot., 34:159–164.

1947b. Studies in the Leguminosae. I. Chromosome numbers in *Erythrina* L. Amer. Journ. Bot., 34:407–414.

Axelrod, D. I.

1952. A theory of angiosperm evolution. Evolution, 6:29–60.

Bailey, I. W.

1944a. The comparative morphology of the Winteraceae. III. Wood. Journ. Arnold Arbor., 25:97–103.

1944b. The development of vessels in angiosperms and its significance in morphological research. Amer. Journ. Bot., 31:421–428.

1949. Origin of the angiosperms: need for a broadened outlook. Journ. Arnold Arbor., 30:64–70.

1951. The use and the abuse of anatomical data in the study of phylogeny and classification. Phytomorphology, 1:67–69.

1953. Evolution of the tracheary tissue of land plants. Amer. Journ. Bot., 40:4–8.

Bailey, I. W., and R. A. Howard

1941. The comparative morphology of the Icacinaceae. Journ. Arnold Arbor., 22:125–132, 171–187, 432–442, 556–568.

Bailey, I. W., and Charlotte G. Nast

1943a. The comparative morphology of the Winteraceae I. Pollen and stamens. Journ. Arnold Arbor., 24:340–346.

1943b. The comparative morphology of the Winteraceae II. Carpels. Journ. Arnold Arbor., 24:472–481.

1945a. The comparative morphology of the Winteraceae VII. Summary and conclusions. Journ. Arnold Arbor., 26:37–47.

1945b. Morphology and relationships of *Trochodendron* and *Tetracentron*. I. Stem, root, and leaf. Journ. Arnold Arbor., 26:143–154.

1948. Morphology and relationships of *Illicium*, *Schisandra*, and *Kadsura*. I. Stem and leaf. Journ. Arnold Arbor., 29:77–89.

Bailey, I. W., Charlotte G. Nast, and A. C. Smith

1943. The family Himantandraceae. Journ. Arnold Arbor., 24:190–206.

Bailey, I. W., and E. W. Sinnott

1914. Investigations on the phylogeny of the angiosperms. No. 2. Anatomical evidences of reduction in certain of the Amentiferae. Bot. Gaz., 58:36–60.

Bailey, I. W., and A. C. Smith

1942. Degeneriaceae, a new family of flowering plants from Fiji. Journ. Arnold Arbor., 23:356–365.

Bailey, I. W., and B. G. L. Swamy

1948. *Amborella trichopoda* Baill., a new morphological type of vesselless dicotyledon. Journ. Arnold Arbor., 29:245–254.

1949. The morphology and relationships of *Austrobaileya*. Journ. Arnold Arbor., 30: 211–226.

1951. The conduplicate carpel of dicotyledons and its initial trends of specialization. Amer. Journ. Bot., 38:373–379.

Bailey, I. W., and W. W. Tupper

1918. Size variation in tracheary cells: I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. Proc. Amer. Acad., 54:149–204.

Baker, H. G.

1948. Dimorphism and monomorphism in the Plumbaginaceae. I. A survey of the family. Ann. Bot., n.s., 12:208–219.

Baker, R. T., and H. G. Smith

1920. A Research on the Eucalyptus Especially in Regard to Their Essential Oils. 2nd ed. xi + 295 pp. Sydney: W. A. Gulick, Government printer.

Baldwin, J. T., Jr.

1940. Cytophyletic analysis of certain annual and biennial Crassulaceae. Madroño, 5:184–192.

Bancroft, H.

1930. The arborescent habit in angiosperms, a review. New Phytol., 29:153–169, 227–275.

Bancroft, Helen

1935. A review of researches concerning floral morphology. Bot. Rev., 1:77–99.

Bancroft, N.

1914. A review of literature concerning the evolution of monocotyledons. New Phytol., 13:285–308.

Barghoorn, E. S., Jr.

1940. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. I. The primitive ray structure. Amer. Journ. Bot., 27:918–928.

1941a. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. II. Modification of the multiseriate and uniseriate rays. Amer. Journ. Bot., 28:273–282.

1941b. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. III. The elimination of rays. Bull. Torrey Club, 68: 317–325.

Baron, W.

1931. Die idealistische Morphologie Al. Brauns und A. P. de Candolles und ihr Verhältnis zur Deszendenzlehre. Beih. Bot. Centr., 48:314–334.

Battaglia, E.

1951. The male and female gametophytes of angiosperms—an interpretation. Phytomorphology, 1:87–116.

Baum, Hermine

1948. Zur Frage des schrittweisen Ueberganges vom apokarpen zum coenokarpen Gynözeum. Oesterr. Bot. Zeitschr., 95:470–474.

1949a. Der einheitliche Bauplan der Angiospermengynözeen und die Homologie ihrer fertilen Abschnitte. Oesterr. Bot. Zeitschr., 96:64–82.

BAUM, HERMINE (Cont.)

1949b. Das Zustandekommen "offener" Angiospermengynözeen. Oesterr. Bot. Zeitschr., 26:285–288.

1949c. Beiträge zur Kenntnis der Schildform bei den Staubblättern. Oesterr. Bot. Zeitschr., 96:453–466.

1950. Unifaziale und subunifaziale Strukturen in Bereich der Blütenhülle und ihre Verwendbarkeit für die Homologisierung der Kelch- und Kronblätter. Oesterr. Bot. Zeitschr., 97:1–43.

BAUMANN, M. G.

1946. *Myodocarpus* und die Phylogenie der Umbelliferen-Frucht; Umbellifloren-Studien I. Ber. Schweiz. Bot. Ges., 56:13–112.

BECHTEL, A. R.

1921. The floral anatomy of the Urticales. Amer. Journ. Bot., 8:386–410.

BELIN-MILLERON, J.

1951. Les théories de la fleur devant la méthodologie. Rev. Scient., 89:36–41.

BELL, C. R.

1954. The *Sanicula crassicaulis* Complex (Umbelliferae); a Study of Variation and Polyploidy. Univ. Calif. Publ. Bot., 27:133–230.

BENSON, L.

1940. The North American subdivisions of *Ranunculus*. Amer. Journ. Bot., 27:799–807.

BENTHAM, G., and J. D. HOOKER

1862–1883. General plantarum ad exemplaria imprimis in herbalis kewensibus servata definita. 3 vols. London: Reeve and Co.

BERRIDGE, E. M.

1914. The structure of the flower of Fagaceae, and its bearing on the affinities of the group. Ann. Bot., 28:509–526.

BERTRAND, P.

1947a. Les végétaux vasculaires; introduction à la l'étude de l'anatomie comparée, suivie de notes originales. 184 pp. Paris: Masson et cie.

1947b. Isolement précose de tous les grande groupes de végétaux vasculaires. Bull. Soc. Bot. France, 84:713–720.

BESSEY, C. E.

1897. Phylogeny and taxonomy of the angiosperms. Bot. Gaz., 24:145–178.

1915. The phylogenetic taxonomy of flowering plants. Ann. Mo. Bot. Gard., 2:109–164.

BEWS, J. W.

1927. Studies in the ecological evolution of the angiosperms. New Phytol., 26:1–21, 65–84, 129–148, 209–248, 273–294.

BIGALKE, HILDEGARD

1933. Die Blattspodograme der Urticaceae und ihre Verwendbarkeit für die Systematik. Beitr. Biol. Pflanz., 21:1–58.

BLAKE, S. F.

1935. Systems of plant classification; a review. Journ. Hered., 26:463–467.

BLASER, H. W.

1941. Studies in the morphology of the Cyperaceae. I. Morphology of flowers. Amer. Journ. Bot., 28:542–551, 832–838.

BLISS, MARY C.

1921. The vessel in seed plants. Bot. Gaz., 71:314–326.

BONDESON, W.

1952. Entwicklungsgeschichte und Bau der Spaltöffnungen bei den Gattungen *Trochodendron* Sieb. et Zucc., *Tetracentron* Oliv. und *Drimys* J. R. et G. Forst. Acta Hort. Berg., 16:169–217.

BOOTHROYD, LUCY E.

1930. The morphology and anatomy of the inflorescence and flower of the Platanaceae. Amer. Journ. Bot., 17:678–693.

BOSCH, E.

1947. Blütenmorphologische und zytologische Untersuchungen an Palmen. Ber. Schweiz. Bot. Ges., 57:37–100.

BOUREAU, E.

1952. L'évolution des végétaux et l'anatomie des plantules. Ann. Biol. III. 56:C. 163–C. 181.

BOYD, LUCY

1930–1931. Evolution in the monocotyledonous seedling: a new interpretation of the morphology of the grass embryo. Trans. and Proc. Bot. Soc. Edinburgh, 30: 286–303.

BREMEKAMP, C. E. B.

1931. The principles of taxonomy and the theory of evolution. Pamphl. So. African Biol. Soc., 4:1–8.

1939. Phylogenetic interpretations and genetic concepts in taxonomy. Chron. Bot., 5:398–403.

BRINK, R. A., and D. C. COOPER

1940. Double fertilization and development of the seed in angiosperms. Bot. Gaz., 102:1–25.

BRITTON, D. M.

1951. Cytogenetic studies on the Boraginaceae. Brittonia, 7:233–266.

BRONGNIART, A.

1843. Énumération des genres des plantes cultivés au Muséum d'Histoire Naturelle de Paris suivant l'orders établi dans l'école de botanique en 1843 par M. Adolphe Brongniart. xxxii + 136 pp. Paris: Fortin, Masson et cie.

BROULAND, M.

1935. Recherches sur l'anatomie florales des Renonculacées. Botaniste, 27:1–276.

BROWN, W. H.

1938. The bearing of nectaries on the phylogeny of flowering plants. Proc. Amer. Philos. Soc., 79:549–594.

BUGNON, P.

1931. Sur le passage effectif de l'état dicotylédone à l'état monocotylédone par hétérocotylie. Bull. Sci. Bourgoyne, 1:13–22.

BUXBAUM, F.

1944. Untersuchungen zur Morphologie der Kakteenblütte. I. Das Gynoeceum. Bot. Archiv, 45:190–247.

CALESTANI, V.

1933. Le origini e la classificazione delle angiosperme. Archivo Bot., 9:274–311.

CAMPBELL, D. H.

1928. The phylogeny of the angiosperms. Bull. Torrey Club, 55:479–497.

1930a. The relationships of *Paulownia*. Bull. Torrey Club, 57:47–50.

1930b. The phylogeny of monocotyledons. Ann. Bot., 44:311–331.

CANDOLLE, A. P. DE

1844. Théorie élémentaire de la botanique; ou, Exposition des principes de la classification naturelle et de l'art de décrire et d'étudier les végétaux. 3rd ed. xii + 468 pp. Paris: Roret.

CANDOLLE, A. P. DE, and K. SPRENGEL

1821. Elements of the Philosophy of Plants: Containing the Principles of Scientific Botany. Transl. from the German. xxxiii + 486 pp. Edinburgh: W. Blackwood.

CANRIGHT, J. E.

1952. The comparative morphology and relationships of the Magnoliaceae. I. Trends of specialization in the stamens. Amer. Journ. Bot., 39:484–497.

CAVE, MARION E.

1941. Megasporogenesis and embryo-sac development in *Calochortus*. Amer. Journ. Bot., 28:390–394.

1948. Sporogenesis and embryo-sac development of *Hesperocallis* and *Leucocrinum* in relation to their systematic position. Amer. Journ. Bot., 35:343–349.

1953. Cytology and embryology in the delimitation of genera. Chron. Bot., 14:140–153.

CHADEFAUD, M.

1936. L'origine cycadéene des angiospermes et la classification générale des phanérogames. Bull. Soc. Bot. France, 83:586–592.

1946. L'origine et l'évolution de l'ovule des phanérogames. Rev. Scient., 84:502–509.

1947. Le pistil des Bennettitales et l'origine des angiospermes. Rev. Scient., 85:938–941.

CHALK, L.

1937. The phylogenetic value of certain anatomical features of dicotyledonous woods. Ann. Bot., n.s., 1:410–428.

1944. The taxonomic value of wood anatomy. Proc. Linn. Soc., 155:214–218.

CHAMBERLAIN, C. J.

1920. The living cycads and the phylogeny of seed plants. Amer. Journ. Bot., 7: 146–153.

CHAPMAN, MARJORIE

1936. Carpel anatomy of the Berberidaceae. Amer. Journ. Bot., 23:340–348.

CHATTAWAY, MARGARET

1932. The wood of the Sterculiaceae. I. Specialization of the vertical wood parenchyma within the sub-family Sterculieae. New Phytol., 31:119–132.

1937. The wood anatomy of the family Sterculiaceae. Philos. Trans. Roy. Soc. London, B 228:313–365.

CHEADLE, V. I.

1937. Secondary growth by means of a thickening ring in certain monocotyledons. Bot. Gaz., 98:535–555.

1938. A preliminary statement on the phylogenetic significance of the anomalous secondary thickening in the Monocotyledoneae. Amer. Journ. Bot., 25:20s. (Abs.)

1939. The occurrence of vessels in the Monocotyledoneae. Amer. Journ. Bot., 26:9s. (Abs.)

Cheadle, V. I. (Cont.)

1942a. The occurrence and types of vessels in the various organs of the plant in the Monocotyledoneae. Amer. Journ. Bot., 29:441–450.

1942b. The role of anatomy in phylogenetic studies of the Monocotyledoneae. Chron. Bot., 7:253–254.

1943a. The origin and certain trends of specialization of the vessel in the Monocotyledoneae. Amer. Journ. Bot., 30:11–17.

1943b. Vessel specialization in the late metaxylem of the various organs in the Monocotyledoneae. Amer. Journ. Bot., 30:484–490.

1944. Specialization of vessels within the xylem of each organ in the Monocotyledoneae. Amer. Journ. Bot., 31:81–92.

1948. Observations on the phloem in the Monocotyledoneae. II. Additional data on the occurrence and phylogenetic specialization in structure of the sieve tubes in the metaphloem. Amer. Journ. Bot., 35:129–131.

Cheadle, V. I., and Natalie W. Uhl

1948. Types of vascular bundles in the Monocotyledoneae and their relation to the late metaxylem conducting elements. Amer. Journ. Bot., 35:486–496.

Cheadle, V. I., and Natalie B. Whitford

1941. A discussion of some factors which influence the form of the vascular bundle in the Monocotyledoneae. Amer. Journ. Bot., 28:2s. (Abs.)

Chester, K. S.

1937. A critique of plant serology. Quart. Rev. Biol., 12:19–46, 165–190, 294–321.

Chorinsky, F.

1931. Vergleichend-anatomische Untersuchung der Haargebilde bei Portucacaceen und Cactaceen. Oesterr. Bot. Zeitschr., 80:308–327.

Chou, Y.-L.

1952. Floral morphology of three species of *Gaultheria*. Bot. Gaz., 114:198–221.

Chute, Hettie M.

1930. The morphology and anatomy of the achene. Amer. Journ. Bot., 17:703–723.

Clausen, J.

1951. Stages in the Evolution of Plant Species. viii + 206 pp. Ithaca: Cornell Univ. Press.

Clausen, P.

1927. Ueber des Verhalten das Antheren-Tapetums bei einigen Monokotylen und Ranales. Bot. Archiv, 18:1–27.

Cockerell, T. D. A.

1935. The origin of the higher flowering plants. Science, 81:458–459.

Constance, L.

1951. The versatile taxonomist. Brittonia, 7:225–231.

1953. The role of plant ecology in biosystematics. Ecology, 34:642–649.

Conzatti, C.

1942. El origen probable de las monocotiledóneas. Proc. 8th Amer. Sci. Congr., 3:197.

Copeland, H. F.

1935a. The structure of the flower of *Pholisma arenarium*. Amer. Journ. Bot., 22:366–383.

1935b. On the genus *Pityopus*. Madroño, 3:154–168.

1937. The reproductive structures of *Pleuriseospora*. Madroño, 4:1–16.

COPELAND, H. F. (Cont.)

1938. The structure of *Allotropa*. Madroño, 4:137–153.

1939. The structure of *Monotropsis* and the classification of the Monotropoideae. Madroño, 5:105–119.

1940. The phylogeny of the angiosperms. Madroño, 5:209–218.

1941. Further studies on Monotropoideae. Madroño, 6:97–122.

1943. A study, anatomical and taxonomic, of the genera of Rhododendroideae. Amer. Midl. Nat., 30:533–625.

1947. Observations on the structure and classification of the Pyroleae. Madroño, 9:65–102.

CORNER, E. J. H.

1946. Centrifugal stamens. Journ. Arnold Arbor., 27:423–437.

1949. The durian theory or the origin of the modern tree. Ann. Bot., n.s., 13:367–414.

1951. The leguminous seed. Phytomorphology, 1:117–150.

COTTON, A. D.

1944. The megaphytic habit in the tree senecios and other genera. Proc. Linn. Soc., 156:158–168.

COULTER, J. M.

1915. The origin of monocotyledony. II. Monocotyledony in grasses. Ann. Mo. Bot. Gard., 2:175–183.

COULTER, J. M., and W. J. G. LAND

1914. The origin of monocotyledony. Bot. Gaz., 57:509–519.

COVAS, G., and B. SCHNACK

1945. El valor taxonomico de la relacion "Longitud del pistilo: Volumen del grano de polen." Darwiniana, 7:80–90.

COX, H. T.

1948a. Studies in the comparative anatomy of the Ericales. I. Ericaceae—sub-family Rhododendroideae. Amer. Midl. Nat., 39:220–245.

1948b. Studies in the comparative anatomy of the Ericales. II. Ericacaceae—sub-family Arbutoideae. Amer. Midl. Nat., 40:493–516.

COY, GEORGIA V.

1928. Morphology of *Sassafras* in relation to phylogeny of angiosperms. Bot. Gaz., 86:149–171.

CROCKER, E. C.

1933. Mäule lignin test on *Podocarpus* wood. Bot. Gaz., 95:168–171.

CROIZAT, L.

1940. A comment on current notions concerning the leaf, stipule and budscale of the angiosperms. Lingnan Sci. Journ., 19:49–66.

1943. The concept of inflorescence. Bull. Torrey Club, 70:496–509.

CROW, W. B.

1926. Phylogeny and the natural system. Journ. Genet., 17:85–155.

CUÉNOD, A.

1932. Hypothèse relative à la place des monocotylédones dans la classification naturelle. Bull. Soc. Bot. France, 79:365–393.

DAHL, A. O.

1952. The comparative morphology of the Icacinaceae, VI. The pollen. Journ. Arnold Arbor., 33:252–295.

DANSER, B. H.

1950. A theory of systematics. Blbl. Biotheor., 4:117–180.

DARLINGTON, C. D.

1939. The Evolution of Genetic Systems. 149 pp. Cambridge: Cambridge Univ. Press.

1952. Évolution et hérédite chez les plantes. Ann. Biol. III. 56:C. 293–C. 300.

DAUMANN, E.

1931a. Zur Phylogenie der Diskusbildungen; Beiträge zur Kenntnis der Nektarien II. Beih. Bot. Centr., 48[1]:183–208.

1931b. Zur morphologischen Wertigkeit der Blütennektarien von *Laurus*. Beih. Bot. Centr., 48[1]:209–213.

DAVY, J. B.

1922. The suffrutescent habit as an adaption to environment. Journ. Ecol., 10:211–219.

1937. On the primary groups of dicotyledons. Ann. Bot., n.s., 1:429–437.

DAWSON, MARION L.

1936. The floral morphology of the Polemoniaceae. Amer. Journ. Bot., 23:501–511.

DEHAY, C.

1941. L'appareil libéro-ligneux foliare des Sterculiacéees. Ann. Sci. Nat., ser. 11, 2:45–131.

DICKSON, JEAN

1936. Studies in floral anatomy. III. An interpretation of the gynaeceum in the Primulaceae. Amer. Journ. Bot., 23:385–393.

DIEHL, G. A.

1935. A study of the Lecythidaceae. Trop. Woods, 43:1–15.

DOMIN, K.

1931. Phylogenetic evolution of the phyllome. Amer. Journ. Bot., 18:237–242.

DORMER, K. J.

1945. An investigation of the taxonomic value of shoot structure in angiosperms with especial reference to Leguminosae. Ann. Bot., n.s., 9:141–153.

1946. Vegetative morphology as a guide to the classification of the Papilionatae. New Phytol., 45:145–161.

DOUGLAS, GERTRUDE E.

1936. Studies in the vascular anatomy of the Primulaceae. Amer. Journ. Bot., 23: 199–212.

1944. The inferior ovary. Bot. Rev., 10:125–186.

DOYEL, BERNICE E., and L. MARGUERITE GOSS

1941. Some details of the reproductive structures of *Sarcodes*. Madroño, 6:1–7.

EAMES, A. J.

1911. On the origin of the herbaceous type in the angiosperms. Ann. Bot., 25:215–224.

1926. The role of flower anatomy in the determination of angiosperm phylogeny. Proc. Internat. Congr. Plant Sci. Ithaca, 1:423–427.

1931. The vacular anatomy of the flower with refutation of the theory of carpel polymorphism. Amer. Journ. Bot., 18:147–188.

1951. Again: "The New Morphology." New Phytol., 50:17–35.

EARLE, T. T.

1938. Embryology of certain Ranales. Bot. Gaz., 100:257–275.

Eber, Erna

1934. Karpellbau und Plazentationsverhältnisse in der Reihe der Helobiae; mit einem Anhang über die verwandtschaftlichen Beziehungen zwischen Ranales und Helobiae. Flora, 127:273–330.

Eckardt, T.

1937. Untersuchungen über Morphologie, Entwicklungsgeschichte und systematische Bedeutung der pseudomonomeren Gynoeceums. Nova Acta Leop.-Carol. (II), 5:1–112.

1938. Das pseudomonomere Gynoeceum. Chron. Bot., 4:206–208.

Edlin, H. L.

1935. A critical revision of certain taxonomic groups of the Malvales. New Phytol., 34:1–20, 122–143.

Edwards, W. N.

1935. The systematic value of cuticular characters in recent and fossil angiosperms. Biol. Rev., 10:442–459.

Eggers, O.

1935. Ueber die morphologische Bedeutung des Leitbündelverlaufes in den Blüten der Rhoeadalen und über das Diagramm der Cruciferen und Capparidaceen. Planta, 24:14–58.

Egler, F. E.

1951. The terminology of floral types. Chron. Bot. 12, Biologia 2:169–173.

Ehrenbergh, L.

1945. Zur Kenntnis der Homologieverhältnisse in der angiospermen Blüte. Bot. Not. 1945:438–444.

Eichler, A. W.

1875. Blüthendiagramme. 2 vols. Leipzig: W. Engelmann.

Elias, M. K.

1946. Taxonomy of Tertiary flowers and herbaceous seeds. Amer. Midl. Nat., 36: 373–380.

Emberger, L.

1949. Les Préphanérogames. Ann. Sci. Nat., ser. 11, 10:131–144.

1950. La valeur morphologique et l'origine de la fleur (á propos d'une théorie nouvelle). Ann. Biol. III, 54:279–296.

1951. L'origine de la fleur. Experientia, 7:161–168.

Endlicher, S.

1836–1840. Genera plantarum secundum ordines naturales disposita. lx + 1483 pp. Vienna: F. Beck.

Engler, A.

1936. Prinzipen der systematischen Anordnung. *In* L. Diels, A. Engler's Syllabus der Pflanzenfamilien. 11th ed. xlii + 419 pp. Berlin: Gebr. Borntraeger.

Erdtman, G.

1943. An Introduction to Pollen Analysis. xvi + 239 pp. Waltham: Chronica Botanica Co.

1953. Pollen Morphology and Plant Taxonomy; Angiosperms. xii + 539 pp. Stockholm: Almquvist and Wiksell.

Erlanson, Eileen W.

1931. A group of tetraploid roses in central Oregon. Bot. Gaz., 91:55–64.

1934. Experimental data for a revision of the North American wild roses. Bot. Gaz., 96:197–259.

Esau, Katherine, V. I. Cheadle, and E. M. Gifford, Jr.

1953. Comparative structure and possible trends of specialization of the phloem. Amer. Journ. Bot., 40:9–19.

Fagerlind, F.

1944. Die tetrasporische Angiospermen-Embryosack und dessen Bedeutung für das Verständnis der Entwicklungsmechanick und Phylogenie des Embryosacks. Arkiv Bot., 31A(11):1–71.

1946. Strobilus und Blüte von Gnetum und die Möglichkeit, aus ihrer Struktur den Blütenbau der Angiospermen zu deuten. Arkiv Bot., 33A(8):1–57.

1948. Beiträge zur Kenntnis der Gynäceummorphologie und Phylogenie der Santalales-Familien. Svensk Bot., Tidskr., 42:195–229.

Fahn, A.

1952. On the structure of floral nectaries. Bot. Gaz., 113:464–470.

Fisher, Mary J.

1928. The morphology and anatomy of the flowers of the Salicaceae. Amer. Journ. Bot., 15:307–326, 372–394.

Foster, A. S.

1931. Phylogenetic and ontogenetic interpretations of the cataphyll. Amer. Journ. Bot., 18:243–249.

1939. Problems of structure, growth and evolution in the shoot apex of seed plants. Bot. Rev., 5:454–470.

1944. Structure and development of sclereids in the petiole of *Camellia japonica* L. Bull. Torrey Club, 71:302–326.

1945. The foliar sclereids of *Trochodendron aralioides* Sieb. & Zucc. Journ. Arnold Arbor., 26:155–162.

1946. Comparative morphology of the foliar sclereids in the genus *Mouriria* Aubl. Journ. Arnold Arbor., 27:253–271.

1950a. Morphology and venation of the leaf in *Quiina acutangula* Ducke. Amer. Journ. Bot., 37:159–171.

1950b. Venation and histology of the leaflets in *Touroulia guianensis* Aubl. and *Froesia tricarpa Pires*. Amer. Journ. Bot., 37:848–862.

1951. Heterophylly and foliar venation in *Lacunaria*. Bull. Torrey Club, 78:382–400.

Fraser, Mabel S.

1937. A study of the vascular supply to the carpels in the follicle-bearing Ranunculaceae. Trans. Roy. Soc. Edinburgh, 59:1–56.

Fries, R. E.

1911. Ein unbeachtet gebliebenes Monokotyledonmerkmal bei einigen Polycarpicae. Ber. Deutsch. Bot. Ges., 29:292–301.

Fritsch, F. E.

1903. The use of anatomical characters for sytsematic purposes. New Phytol., 2: 177–184.

Fritsch, K.

1905. Die Stellung der Monokotylen im Pflanzensystem. Bot. Jahrb. 34, Beibl. 79, pp. 22–40.

1932. Die systematische Gruppierung der Monokotylen. Ber. Deutsch. Bot. Ges., 50a: 162–184.

Frost, F. H.

1930a. Specialization in secondary xylem of dicotyledons. I. Origin of vessel. Bot. Gaz., 89:67–94.

1930b. Specialization in secondary xylem of dicotyledons. II. Evolution of end wall of vessel segment. Bot. Gaz., 90:198–212.

1931. Specialization in secondary xylem of dicotyledons. III. Specialization of lateral wall of vessel segment. Bot. Gaz., 91:88–96.

Garratt, G. A.

1933a. Systematic anatomy of the woods of the Myristicaceae. Trop. Woods, 35:6–48.

1933b. Bearing of wood anatomy on the relationships of the Myristicaceae. Trop. Woods, 36:20–44.

1934. Systematic anatomy of the woods of the Monimiaceae. Trop. Woods, 39:18–44.

Gaussen, P.

1952. L'évolution pseudocyclique. Ann. Biol. III, 56:C. 207–C. 220.

Gauthier, R.

1950. The nature of the inferior ovary in the genus *Begonia*. Contr. Inst. Bot. Univ. Montréal, 66:5–91.

George, L.

1931. Les rapports des Gnétales aves lec dicotylédones et les gymnospermes. Compt. Rend. Acad. Sci. Paris, 193:1451–1453.

Gertz, O.

1943. Zur Kenntnis der Holzreaktion nach Mäule; einschliesslich einige phylogenetische Bermerkungen. Bot. Not., 1943:203–218.

Gibbs, R. D.

1945. Comparative chemistry as an aid to the solution of problems in systematic botany. Trans. Roy. Soc. Canada, ser. 3, 39(5):71–103.

Gilbert, S. G.

1940. Evolutionary significance of ring porosity in woody angiosperms. Bot. Gaz., 102:105–120.

Gilg, E., and P. N. Schürhoff

1926. Die Serodiagnostik in der botanischen Verwandtschaftsforschung. Bot. Jahrb., 60:439–450.

Gilmour, J. S. L.

1940. Taxonomy and philosophy. *In* J. Huxley, New Systematics, pp. 461–474.

Gilmour, J. S. L., *et al.*

1940. A discussion of phylogeny and taxonomy. Proc. Linn. Soc., 152:234–255.

Gilmour, J. S. L., and W. B. Turrill .

1941. The aim and scope of taxonomy. Chron. Bot., 6:217–219.

Gleason, H. A.

1952. Some fundamental concepts in taxonomy. Phytologia, 4:1–20.

Glišić, Ljubeša M.

1929. Ueber die Endosperm- und Haustorienbildung bei *Orobanche hederae* Duby und *Orobanche gracilis* Sm. (Zugleich ein Beitrag zur Phylogenie der Orobanchaceae). Bull. Inst. and Jard. Bot. Univ. Belgrade, 1:106–141.

Glück, H.

1919. Blatt- und blütenmorphologische Studien; ein morphologische Untersuchung über die Stipulargebilde, über die Intravaginalpapillen, über die Blattscheide

Glück, H. (Cont.)
und über die Bewertung der Blütenblattgebilde. xxiii + 696 pp. Jena: G. Fischer.
1925. Kritische Bemerkungen über die phylogenetische Herkunft der Monokotylen. Flora, 118/119:150–164.

Granick, Elsa B.
1944. A karyosystematic study of the genus *Agave*. Amer. Journ. Bot., 31:283–293.

Grant, V.
1949. Pollination systems as isolating mechanisms in angiosperms. Evolution, 3:82–97.
1950a. The flower constancy of bees. Bot. Rev., 16:379–398.
1950b. The protection of the ovules in flowering plants. Evolution, 4:179–201.
1950c. The pollination of *Calycanthus occidentalis*. Amer. Journ. Bot., 37:294–297.
1952. Isolation and hybridization between *Aquilegia formosa* and *A. pubescens*. El Aliso, 2:341–360.

Gray, A.
1893. Letters of Asa Gray. Jane Loring Gray, ed. 2 vols. Boston and New York: Houghton, Mifflin and Co.; Cambridge: Riverside Press.

Green, J. R.
1914. A History of Botany in the United Kingdom from the Earliest Times to the End of the 19th Century. xii + 648 pp. London and Toronto: J. M. Dent and Sons; New York: E. P. Dutton and Co.

Grégoire, V.
1931. La valeur morphologique des carpelles dans les angiosperms. Bull. Acad. Roy. Belgique Sci. V, 17:1286–1302.
1938. La morphogénèse et l'autonomie morphologique de l'appareil floral. 1. Le carpelle. Cellule, 47:287–452.

Gregory, W. C.
1941. Phylogenetic and cytological studies in the Ranunculaceae. Trans. Amer. Philos. Soc. II., 31:442–520.

Gunderson, A.
1939a. Flower buds and phylogeny of dicotyledons. Bull. Torrey Club, 66:287–295.
1939b. The classification of dicotyledons. Torreya, 39:108–111.
1941. Flower structure and the classification of dicotyledons. Brooklyn Bot. Gard. Rec., 30:93–98.
1943. Flower forms and groups of dicotyledons. Bull. Torrey Club, 70:510–516.

Gupta, K. M.
1934. On the wood anatomy and theoretical significance of homoxylous angiosperms. Journ. Indian Bot. Soc., 13:71–101.

Guşuleac, M.
1938a. Der genetische Standpunkt in der Taxonomie der Früchte. Bul. Fac. Stiinte Cernauti, 12:206–219.
1938b. Zur Präzisierung der Nomenklatur der Früchte und der Prinzipien eines natürlichen Fruchtsystems. Bul. Fac. Stiinte Cernauti, 12:337–355.

Haan, H. R. M. de
1920. Contribution to the knowledge of the morphological value and the phylogeny of the ovule and its integuments. Rec. Trav. Bot. Néerl., 17:219–324.

Haccius, Barbara
1939. Untersuchungen über die Bedeutung des Distichie für das Verständnis der zerstreuten Blattstellung bei den Dikotylen. Bot. Archiv, 40:58–159.

HAGERUP, O.

1930. Vergleichende morphologische und systematische Studien über die Ranken und andere vegetative Organe der Cucurbitaceen und Passifloraceen. Dansk Bot. Ark., 6(8):1–103.

1938. On the origin of some angiosperms through the Gnetales and the Coniferae. III. The gynaecium of *Salix cinerea*. K. Danske Vidensk. Selsk. Biol. Meddel., 14(4):1–34.

1942. The morphology and biology of the *Corylus*-fruit. K. Danske Vidensk. Selsk. Biol. Meddel., 17(6):1–32.

HALL, B. A.

1951. The floral anatomy of the genus *Acer*. Amer. Journ. Bot., 38:793–799.

HALL, H. M.

1928. The genus *Haplopappus*, a Phylogenetic Study in the Compositae. Carnegie Inst. Washington Publ. 389. viii + 391 pp.

HALL, J. W.

1952. The comparative anatomy and phylogeny of the Betulaceae. Bot. Gaz., 113: 235–270.

HALLIER, H.

1905. Provisional scheme of the natural (phylogenetic) system of flowering plants. New Phytol., 4:151–162.

1912. L'origine et le système phylétique des angiospermes exposés à l'aide de leur arbre généalogique. Arch. Néerl. Sci. Exact. et Nat., ser. IIIB, 1:146–234.

HALLOCK, FRANCES A.

1930. The relationship of *Garrya;* the development of the flower and seeds of *Garrya* and its bearing on the phylogenetic position of the genus. Ann. Bot., 44: 771–812.

HAMMEN, L. VAN DER

1948. Traces of ancient dichotomies in angiosperms (a contribution to our knowledge of phyllospory and stachyspory). Blumea, 6:290–301.

HARE, C. L.

1944. The anatomy of the petiole and its taxonomic value. Proc. Linn. Soc., 155: 223–229.

HARRIS, T. M.

1940. *Caytonia*. Ann. Bot., ser. 2, 4:713–734.

1951a. *Caytonanthus*, the microsporophyll of *Caytonia*. Ann. Bot., ser. 2, 5:47–58.

1951b. The relationships of the Caytoniales. Phytomorphology, 1:29–39.

HAYATA, B.

1921. The natural classification of plants according to the dynamic system. Icones plantarum formosanarum, 10:97–234.

1931. Ueber das "dynamische System" der Pflanzen. Ber. Deutsch. Bot. Ges., 49: 328–348.

HEDBERG, O.

1946. Pollen morphology in the genus *Polygonum* L. s. lat. and its taxonomical significance. Svensk Bot., Tidskr., 40:371–404.

HEIMSCH, C., JR.

1938. The significance of anatomy in taxonomic studies in the Juglandaceae. Amer. Journ. Bot., 25:20s. (Abs.)

HEIMSCH, C. JR. (Cont.)

1940. Wood anatomy and pollen morphology of *Rhus* and allied genera. Journ. Arnold Arbor., 27:279–291.

1942. Comparative anatomy of the secondary xylem in the "Gruinales" and "Terebinthales," of Wettstein with reference to taxonomic grouping. Lilloa, 8:83–198.

HEIMSCH, C., and R. H. WETMORE

1939. The significance of wood anatomy in the taxonomy of the Juglandaceae. Amer. Journ. Bot., 26:651–660.

HEINIG, KATHERINE H.

1951. Studies in the floral morphology of the Thymelaeceae. Amer. Journ. Bot., 38: 113–132.

HEINTZELMAN, C. E., JR., and A. A. HOWARD

1948. A comparative morphology of the Icacinaceae, V. The pubescence and the crystals. Amer. Journ. Bot., 35:42–52.

HEMENWAY, A. F.

1911. Studies on the phloem of the dicotyledons. I. Phloem of the Juglandaceae. Bot. Gaz., 51:131–135.

1913. Studies on the phloem of the dicotyledons. II. The evolution of the sieve-tube. Bot. Gaz., 55:236–243.

HENSLOW, G.

1893. A theoretical origin of endogens from exogens, through self-adaptation to an aquatic habit. Journ. Linn. Soc., 29:485–528.

1911. The origin of monocotyledons from dicotyledons through self-adaptation to a moist or aquatic habit. Ann. Bot., 25:717–744.

HILDITCH, T. P.

1940. The Chemical Constitution of Natural Fats. xi + 437 pp. New York: Wiley and Sons.

1952. The seed and fruit fats of plants: Endeavour, 11:173–182.

HILL, A. W.

1906. The morphology and seedling structure of the geophilous species of *Peperomia*, together with some views on the origin of monocotyledons. Ann. Bot., 20: 395–427.

HIRMER, M.

1935. Die Pteridospermae, insbesondere die Caytoniales und die Entwickelung der Angiospermae. Proc. 6th Internat. Bot. Congr. Amsterdam, 2:231–234.

HJELMQVIST, H.

1948. Studies on the floral morphology and phylogeny of the Amentiferae. Bot. Not. Suppl., 2(1):5–171.

HOAR, C. S.

1916. The anatomy and phylogenetic position of the Betulaceae. Amer. Journ. Bot., 3:415–435.

HOLDEN, RUTH

1912. Reduction and reversion in the North American Salicales. Ann. Bot., 26:165–173.

HOOKER, J. D.

1873. The orders arranged after the method followed in the universities and schools of Great Britain, its colonies, America, and India; with additions, an appen-

HOOKER, J. D. (Cont.)
dix on the natural method and a synopsis of the orders. *In* E. Le Maout and J. Decaisne, A General System of Botany. Transl. by Frances E. Hooker. xii + 1066 pp. London: Longmans, Green and Co.

HSÜ, J., and M. N. BOSE
1952. Further information on *Homoxylon rajmahalense* Sahni. Journ. Indian Bot. Soc., 31:1–12.

HUNT, K. W.
1937. A study of the style and stigma, with reference to the nature of the carpel. Amer. Journ. Bot., 24:288–295.

HUTCHINSON, J.
1923–1924. Contributions towards a phylogenetic classification of flowering plants. I. Kew Bull., 1923:65–89; IV. *Ibid.*, 1924:114–134.
1926. The Families of Flowering Plants, Arranged According to a New System Based on Their Probable Phylogeny. Vol. I. Dicotyledons. xiv + 328 pp. London: Macmillan and Co.
1929. The phylogeny of flowering plants. Proc. Internat. Congr. Plant Sci. Ithaca, 1:413–421.
1934. The Families of Flowering Plants, Arranged According to a New System Based on Their Probable Phylogeny. Vol. II. Monocotyledons. xiii + 243 pp. London: Macmillan and Co.
1935. A new phylogenetic classification of monocotyledons. Proc. 6th Internat. Bot. Congr. Amsterdam, 2:129–131.

HUTCHINSON, J. B.
1947. Notes on the classification and distribution of genera related to *Gossypium*. New Phytol., 46:123–141.

HUXLEY, J. S.
1940. Towards the new systematics. *In* J. Huxley, New Systematics, pp. 1–46.

HUXLEY, L.
1918. Life and Letters of Sir Joseph Dalton Hooker, O.M., G.C.S.I., Based on Materials Collected and Arranged by Lady Hooker. 2 vols. x + 546 pp; vi + 569 pp. London: John Murray.

JACKSON, GEMMA
1934. The morphology of the flowers of *Rosa* and certain closely related genera. Amer. Journ. Bot., 21:453–466.

JAEGER, P.
1950. Nectaires floraux et phylogénèse. Ann. Biol. III, 54:111–117.

JANCHEN, E.
1932. Entwurf eines Stammbaumes der Blütenpflanzen nach Richard Wettstein. Oesterr. Bot. Zeitschr., 81:161–166.
1950. Die Herkunft der Angiospermen-Blüte und die systematische Stellung der Apetalen. Oesterr. Bot. Zeitschr., 97:129–167.

JEFFREY, E. C., and R. E. TORREY
1921. Physiological and morphological correlations in herbaceous angiosperms. Bot. Gaz., 71:1–31.

JOHANSEN, D. A.
1950. Plant Embryology; Embryogeny of the Spermatophyta. xvi + 305 pp. Waltham: Chronica Botanica Co.

JOHNSTON, I. M.

1952. Studies in the Boraginaceae, XXIII. A survey of the genus *Lithospermum*. Journ. Arnold Arbor., 33:299–363.

JOSHI, A. C.

1938. Systematic distribution of the *Fritillaria*-type of embryo sac and the mono- or polyphyletic origin of angiosperms. Chron. Bot., 4:507–508.

1946. A note on the development of pollen of *Myristica fragrans* Van Houtte and the affinities of the family Myristicaceae. Journ. Indian Bot. Soc., 25:139–143.

1947. Floral histogenesis and carpel morphology. Journ. Indian Bot. Soc., 26:63–74.

JUHNKE, GERDA, and H. WINKLER

1938. Der Balg als Grundelment des Angiospermengynaeceums. Beitr. Biol. Pflanz., 25:290–324.

JUNELL, S.

1934. Zur Gynäceummorphologie und Systematik der Verbenaceen und Labiaten Symbol. Bot. Upsal., 4:1–219.

JUSSIEU, A. DE

1850. Course élémentaire d'histoire naturelle botanique. vii + 552 pp. Paris: Langlois and Leclercq, V. Masson.

JUST, T.

1946. The use of embryological formulas in plant taxonomy. Bull. Torrey Club, 73: 351–355.

1948. Gymnosperms and the origin of angiosperms. Bot. Gaz., 110:91–103.

1952. Origine et évolution de la fleur. Ann. Biol. III, 56:C. 135–C. 143.

KARSTEN, G.

1918. Zur Phylogenie der Angiospermen. Zeitschr. Bot., 10:369–388.

KASAPLIGIL, B.

1951. Morphological and ontogenetic studies of *Umbellularia californica* Nutt. and *Laurus nobilis* L. Univ. Calif. Publ. Bot., 25:115–240.

KAUSIK, S. B.

1938a. Studies in the Proteaceae. II. Floral anatomy and morphology of *Macadamia ternifolia* F. Muell. Proc. Indian Acad. Sci., 8(B):45–62.

1938b. Studies in the Proteaceae. I. Cytology and floral morphology of *Grevillea robusta*. Cunn. Ann. Bot., n.s., 2:899–910.

KAUSSMANN, B.

1941. Vergleichende Untersuchungen über die Blattnatur der Kelch-, Blumen- und Staubblätter. Bot. Archiv, 42:503–572.

KAVALJIAN, L. G.

1952. The floral morphology of *Clethra alnifolia* with some notes on *C. acuminata* and *C. arborea*. Bot. Gaz., 113:392–413.

KNOLL, F.

1939. Ueber den Begriff "Frucht." Biologe, 8:154–160.

KOCH, MINNA F.

1930. Studies in the anatomy and morphology of the Composite flower. Amer. Journ. Bot., 17:938–952, 995–1010.

KOZO-POLJANSKI, B.

1936. On some "third" conceptions in floral morphology. New Phytol., 35:479–492.

KRATZER, J.

1918. Die verwandtschaftlichen Beziehungen der Cucurbitaceen auf Grund ihrer Samenentwicklung. Flora, 110:275–343.

KRIBS, D. A.

1930. Comparative anatomy of the woods of the Meliaceae. Amer. Journ. Bot., 17: 724–738.

1935. Salient lines of structural specialization in the wood rays of dicotyledons. Bot. Gaz., 96:547–557.

1937. Salient lines of structural specalization in the wood parenchyma of dicotyledons. Bull. Torrey Club, 64:177–186.

KROHN, V.

1935. Eine kritische Nachprüfung der Sympetalen des Königsberger serodiagnostischen Stammbaums. Bot. Archiv, 37:328–372.

KÜHN, GERTRUD

1928. Beiträge zur Kenntnis der intraseminalen Leitbündel bei den Angiospermen. Bot. Jahrb., 61:325–379.

KUMAZAWA, M.

1930. Studies on the structure of Japanese species of *Ranunculus*. Journ. Fac. Sci. Tokyo Imp. Univ., sec. 3 (Bot.), 2:297–343.

LAM, H. J.

1936. Phylogenetic symbols, past and present (being an apology for genealogical trees). Acta Biotheor., 2:153–194.

1948a. Classification and the new morphology. Acta Biotheor., 8:107–154.

1948b. A new system of the cormophyta. Blumea, 6:282–289.

1950. Stachyspory and phyllospory as factors in the natural system of the cormophyta. Svensk Bot. Tidskr., 44:517–534.

1952. L'évolution des plantes vasculaires. Ann. Biol. III, 56:C. 57–C. 84.

LANGDON, LADEMA M.

1939. Ontogenetic and anatomical studies of the flower and fruit of the Fagaceae and Juglandaceae. Bot. Gaz., 101:301–327.

1947. The comparative morphology of the Fagaceae. I. The genus *Nothofagus*. Bot. Gaz., 108:350–371.

LAUBENGAYER, R. A.

1937. Studies in the anatomy and morphology of the Polygonaceous flower. Amer. Journ. Bot., 24:329–343.

LAWRENCE, G. H. M.

1951. Taxonomy of Vascular Plants. xii + 823 pp. New York: Macmillan and Co.

1952. Morphology and the taxonomist. Phytomorphology, 2:30–34.

LAWRENCE, JULIA R.

1937. A correlation of the taxonomy and the floral anatomy of certain of the Boraginaceae. Amer. Journ. Bot., 24:433–444.

LAWRENCE, W. J. C., J. R. PRICE, GERTRUDE M. and R. ROBINSON

1939. The distribution of anthocyanins in flowers, fruits and leaves. Philos. Trans. Roy. Soc. London, B 230:149–178.

LEANDRI, J.

1930. Recherches anatomiques sur les Thyméleacées. Ann. Sci. Nat., ser. 10, 12: 125–237.

LEINFELLNER, W.

1940. Das epidermale Randwachstum der Fruchtblätter. Bot. Archiv, 40:507–515.

1941. Ueber den unterständigen Fruchtknoten und einige Bemerkungen über den Bauplan des verwachsenblättrigen Gynoeceums an sich. Bot. Archiv, 42:1–43.

1950. Der Bauplan des synkarpen Gynözeums. Oesterr. Bot. Zeitschr., 97:403–436.

1951. Die U-förmige Plazenta als der Plazentationstypus der Angiospermen. Oesterr. Bot. Zeitschr., 98:338–358.

LEITNER, JOSEFINE

1942. Ein Beitrag zu Kenntnis der Pollenkörner der Labiatae. Oesterr. Bot. Zeitschr., 91:29–40.

LESMESLE, R.

1946a. Les divers aspects de fibres à ponctuations aréolées chez les Apocarpées archaïques et la critérium de la trachéide du type cycadéen. Compt. Rend. Acad. Sci. Paris, 222:195–196.

1946b. Les divers types de fibres à ponctuations aréolées chez les dicotyledones apocarpiques les plus archaïques et leur rôle dans la phylogénie. Ann. Sci. Nat., ser. 11, 7:19–40.

1946c. Contribution a l'étude morphologique et phylogénétique des Euptéleacées, Cercidophyllacées, Eucommiacées (ex-Trochodendracées). Ann. Sci. Nat., ser. 11, 7:41–52.

1948. Trachéides aréolées du type cycadéen dans le genre *Paconia;* leur intérêt au point de vue systématique et phylogénétique. Compt. Rend. Acad. Sci. Paris, 226:2172–2173.

1953. Nature des éléments sclérenchymateaux de la tige du *Lactoris fernandeziana* Philippi. Rev. Gén. Bot., 60:15–21.

LEWIS, D.

1942. The evolution of sex in flowering plants. Biol. Rev., 17:46–67.

LI, H.-L.

1951. Evolution in the flowers of *Pedicularis.* Evolution, 5:158–164.

LIEHR, O.

1916. Ist die angenommene Verwandtschaft der Helobiae und Polycarpicae auch in ihrer Cytologie zu erkennen? Beitr. Biol. Pflanz., 13:135–220.

LIGNIER, M. O.

1908. Le fruit des Bennettitées et l'ascendance des angiospermes. Mém. Bot. Soc. France, 13:1–17.

LINDINGER, L.

1910. Bemerkungen zur Phylogenie der Monokotylen. Naturwiss. Wochenschr. II, 9:65–71.

LINDLEY, J.

1830. An Introduction to the Natural System of Botany: or a Systematic View of the Organisation, Natural Affinities, and Geographical Distribution, of the Whole Vegetable Kingdom. xlviii + 374 pp. London: Longman, Rees, Orme, Brown, and Green.

LINDSEY, A. A.

1938. Anatomical evidence for the Menyanthaceae. Amer. Journ. Bot., 25:480–485.

1940. Floral anatomy in the Gentianaceae. Amer. Journ. Bot., 27:640–652.

LOTSY, J. P.

1911. Vorträge über botanische Stammesgeschichte; ein Lehrbuch der Pflanzensystematik. 3 vols. Jena: G. Fischer.

LYON, H. L.
1905. The embryo of the angiosperms. Amer. Nat., 39:13–35.

MACDUFFIE, R. C.
1921. Vessels of the Gnetalean type in angiosperms. Bot. Gaz., 71:438–445.

MAHESHWARI, P.
1937. A critical review of the types of embryo sacs in angiosperms. New Phytol., 36:359–417.
1939. Are the angiosperms polyphyletic? Chron. Bot., 5:417–418.
1945. The place of angiosperm embryology in research and teaching. Journ. Indian Bot. Soc., 24:25–41.
1948. The angiosperm embryo sac. Bot. Rev., 14:1–56.
1949. The male gametophyte of angiosperms. Bot. Rev., 15:1–75.
1950. An Introduction to the Embryology of Angiosperms. x + 453 pp. New York: McGraw-Hill.

MANGENOT, G.
1952. L'évolution de l'ovule du pistil et du fruit. Ann. Biol., ser. 3, 56:C. 149–C. 162.

MANNING, W. E.
1938. The morphology of the flowers of the Juglandaceae. I. The inflorescence. Amer. Journ. Bot., 25:407–419.
1940. The morphology of the flowers of the Juglandaceae. II. The pistillate flowers and fruit. Amer. Journ. Bot., 27:839–852.
1948. The morphology of the flowers of the Juglandaceae. III. The staminate flowers. Amer. Journ. Bot., 35:606–621.

MARKGRAF, F.
1936. Blütenbau und Verwandtschaft dei den einfachsten Helobiae. Ber. Deutsch. Bot. Ges., 54:191–229.

MARTENS, P.
1947. Le graine et le tube pollinique; réflexions sur les caractères des phanérogames. Bull. Acad. Roy. Belgique Sci., ser. 5, 33:919–943.
1951. Les Préphanérogames et le probléme de la graine. Cellule, 54:103–132.

MARTIN, A. C.
1946. The comparative internal morphology of seeds. Amer. Midl. Nat., 36:513–660.

MASON, H. L.
1950. Taxonomy, systematic botany, and biosystematics. Madroño, 10:193–208.

MATTFIELD, J.
1938a. Das morphologische Wesen und die phylogenetische Bedeutung der Blumenblätter. Ber. Deutsch. Bot. Ges., 56:86–116.
1938b. Ueber eine angebliche *Drymaria* Australiens nebst Bemerkungen über die Staminaldrüsen und die Petalen der Caryophyllaceen. Beih. Repert. Sp. Nov., 100:149–164.

MATTHEWS, J. R.
1941. Floral morphology and its bearing on the classification of angiosperms. Trans. and Proc. Bot. Soc. Edinburgh, 33:69–82.

MATTHEWS, J. R., and E. M. KNOX
1926. The comparative morphology of the stamen in the Ericaceae. Trans. and Proc. Bot. Soc. Edinburgh, 29:243–281.

Matthews, J. R., and C. M. MacLachlan

1929. The structure of certain porocidal anthers. Trans. and Proc. Bot. Soc. Edinburgh, 30:104–122.

Mauritzon, J.

1933. Studien über die Embryologie der Familien Crassulaceae und Saxifragaceae. (Thesis.) Lund.

1934. Ein Beitrag zur Embryologie der Phytolaccaceen und Cactaceen. Bot. Not., 1934:111–135.

McKelvey, Susan D., and K. Sax

1933. Taxonomic and cytological relationships of *Yucca* and *Agave*. Journ. Arnold Arbor., 14:76–81.

McLaughlin, R. P.

1933. Systematic anatomy of the wood of the Magnoliales. Trop. Woods, 34:3–39.

McLean, R. C., and M. Evans

1934. The Mäule reaction and the systematic position of the Gnetales. Nature, 134: 936–937.

McNair, J. B.

1934. The evolutionary status of plant families in relation to some chemical properties. Amer. Journ. Bot., 21:427–452.

1935a. The taxonomic and climatic distribution of alkaloids. Bull. Torrey Club, 62: 219–226.

1935b. Angiosperm phylogeny on a chemical basis. Bull. Torrey Club, 62:515–532.

1942. Some chemical properties of *Eucalyptus* in relation to their evolutionary status. Madroño, 6:181–190.

1945a. Plant fats in relation to environment and evolution. Bot. Rev., 11:1–59.

1945b. Some comparisons of chemical ontogeny with chemical phylogeny in vascular plants. Lloydia, 8:145–169.

Melchior, H.

1932. Blütenstandsbildung bei der Gattung *Viola;* ein Beitrag zur Phylogenie der Violaceen. Ber. Deutsch. Bot. Ges., 50:198–204.

Metcalfe, C. R.

1944. An introduction, with special reference to the anatomy of the leaf and stem. *In* symposium, On the taxonomic value of the anatomical structure of the vegetative organs of the dicotyledons. Proc. Linn. Soc., 155:210–214.

1946. The systematic anatomy of the vegetative organs of the angiosperms. Biol. Rev., 21:159–172.

Metcalfe, C. R., and L. Chalk

1950. Anatomy of the Dicotyledons; Leaves, Stem, and Wood in Relation to Taxonomy, with Notes on Economic Uses. 2 vols. Oxford: Clarendon Press.

Meyer, F. J.

1932. Die Verwandtschaftsbeziehungen der Alismataceen zu den Ranales in Lichte der Anatomie. Bot. Jahrb., 65:53–59.

Mez, C.

1936. Morphologie und Serodiagnostik, erläutert an Blüte und Blütenstand, vom Irreversibilitätsgesetz ausgesehen. Bot. Archiv, 38:86–104.

Mez, C., and H. Ziegenspeck

1926. Der Königsberger serodiagnostische Stammbaum. Bot. Archiv, 13:483–486.

MONEY, LILLIAN L., I. W. BAILEY, and B. G. L. SWAMY

1950. The morphology and relationships of the Monimiaceae. Journ. Arnold Arbor., 31:372–404.

MOORE, J. A.

1936a. The vascular anatomy of the flower in the papilionaceous Leguminosae. Amer. Journ. Bot., 23:279–290, 349–355.

1936b. Floral anatomy and phylogeny in the Rutaceae. New Phytol., 35:318–322.

MOORE, R. J.

1948. Cytotaxonomic studies in the Loganiaceae. II. Embryology of *Polypremum procumbens* L. Amer. Journ. Bot., 35:404–410.

MORITZ, O.

1929. Betrachtungen zum "Ende" der botanischen Serodiagnostik. Beih. Bot. Centr., 46(2):114–118.

1934. Die botanische Serologie. Beitr. Biol. Pflanz., 22:51–90.

MORLEY, T.

1953a. The genus *Mouriri* (Melastomaceae); a sectional revision based on anatomy and morphology. Univ. Calif. Publ. Bot., 26:223–312.

1953b. A new genus and three new species in the Memecyleae (Melastomaceae). Amer. Journ. Bot., 40:248–255.

MOSELEY, M. F., JR.

1948. Comparative anatomy and phylogeny of the Casuarinaceae. Bot. Gaz., 110: 231–280.

MOYER, L. S.

1934a. Species relationships in *Euphorbia* as shown by the electrophoresis of latex. Amer. Journ. Bot., 21:293–313.

1934b. Electrophoresis of latex and chromosome numbers of poinsettias. Bot. Gaz., 95: 678–685.

1936. Chromosome number and electrophoresis of latex in *Asclepias*. Bot. Gaz., 97: 860–865.

MÜNTZING, A.

1936. The evolutionary significance of autopolyploidy. Hereditas, 21:263–378.

MURLEY, MARGARET R.

1951. Seeds of the Cruciferae of northeastern North America. Amer. Midl. Nat., 46:1–81.

NAGARAJ, M.

1952. Floral morphology of *Populus deltoides* and *P. tremuloides*. Bot. Gaz., 114: 222–243.

NAST, CHARLOTTE G.

1944. The comparative morphology of the Winteraceae VI. Vascular anatomy of the flowering shoot. Journ. Arnold Arbor., 25:454–466.

NAST, CHARLOTTE G., and I. W. BAILEY

1945. Morphology and relationships of *Trochodendron* and *Tetracentron*, II. Inflorescence, flower, and fruit. Journ. Arnold Arbor., 26:267–276.

1946. Morphology of *Euptelea* and comparison with *Trochodendron*. Journ. Arnold Arbor., 27:186–192.

NETOLITZKY, F.

1926. Anatomie der Angiospermen-Samen. *In* K. Linsbauer, Handbuch der Pflanzenanatomie, 10(1):iv + 364 pp.

NEUMANN, MARGARETE

1935. Die Entwicklung des Pollens, der Samenanlage und des Embryosackes von *Pereskia amapola* var. *argentina*. Oesterr. Bot. Zeitschr., 84:1–30.

NEUMAYER, H.

1924. Die Geschichte der Blüte. Abh. Zool.-Bot. Ges. Wien, 14(1):1–110.

NICOTRA, L.

1909–1910. Sur le système des monocotyldédonées. Oesterr. Bot. Zeitschr., 59:15–19; 60:309–307.

NITZSCHKE, J.

1914. Beiträge zur Phylogenie der Monokotylen, gegründet auf der Embryosackentwicklung apokarper Nymphaeaceen und Helobien. Beitr. Biol. Pflanz., 12: 223–267.

NORRIS, T.

1941. Torus anatomy and nectary characteristics as phylogenetic criteria in the Rhoeadales. Amer. Journ. Bot., 28:101–113.

ODELL, M. E.

1932. The determination of fossil angiosperms by the characteristics of their vegetative organs. Ann. Bot., 46:941–963.

OZENDA, P.

1946. La nature morphologique du carpelle. Rev. Scient., 84:393–404.

1949. Récherches sur les dicotylédones apocarpiques; contribution à l'étude des angiospermes dites primitives. École Normale Supér. Publ. Lab. Biol., 183 pp. Paris.

1952. Remarques sur quelques interprétations de l'étamine. Phytomorphology, 2: 225–231.

PALSER, BARBARA F.

1951. Studies of floral morphology in the Ericales. I. Organography and vascular anatomy in the Andromedeae. Bot. Gaz., 112:447–485.

1952. Studies of floral morphology in the Ericales. II. Megasporogenesis and megagametophyte development in the Andromedeae. Bot. Gaz., 114:33–52.

PARKIN, J.

1914. The evolution of the inflorescence. Journ. Linn. Soc., 42:511–563.

1923. The strobilus theory of angiospermous descent. Proc. Linn. Soc., 135:51–64.

1951. The protrusion of the connective beyond the anther and its bearing on the evolution of the stamen. Phytomorphology, 1:1–8.

1952. The unisexual flower—a criticism. Phytomorphology, 2:75–79.

PENNELL, F. W.

1948. The taxonomic significance of an understanding of floral evolution. Brittonia, 6:301–308.

PERRY, B. A.

1943. Chromosome number and phylogenetic relationships in the Euphorbiaceae. Amer. Journ. Bot., 30:527–543.

PHILIPSON, W. R.

1946. Studies in the development of the inflorescence. I. The capitulum of *Bellis perennis* L. Ann. Bot., n.s., 10:257–270.

1947a. Studies in the development of the inflorescence. II. The capitula of *Succisia pratensis* Moench and *Dipsacus fullonum* L. Ann. Bot., n.s., 11:285–297.

PHILIPSON, W. R. (Cont.)

1947b. Studies in the development of the inflorescence. III. The thyrse of *Valeriana officinalis* L. Ann. Bot., n. s., 11:409–416.

1948a. Studies in the development of the inflorescence. IV. The capitula of *Hieracium boreale* Fries and *Dahlia gracilis* Ortg. Ann. Bot., n.s., 12:65–75.

1948b. Studies in the development of the inflorescence. V. The raceme of *Lobelia Dortmanna* L., and other Campanulaceous inflorescences. Ann. Bot., n.s., 12:147–156.

1949. The ontogeny of the shoot apex in dicotyledons. Biol. Rev., 24:21–50.

PLANTEFOL, L.

1947. Une théorie phyllotaxique nouvelle: hélices foliares multiples et contiguïte. Rev. Scient., 85:343–356.

1949. L'ontogénie de la fleur; fondements d'une théorie florale nouvelle. Ann. Sci. Nat., ser. 11, 9:33–186.

PODDUBNAJA-ARNOLDI, W.

1931. Ein Versuch der Anwendung der embryologischen Methode bei der Lösung einiger systematischer Fragen. I. Vergleichende embryologisch-zytologische Untersuchungen über der Gruppe Cynareae, Fam. Compositae. Beih. Bot. Centr., 48(2):141–237.

POHL, F.

1928. Der einfaltige Pollen, seine Verbreitung und phylogenetische Bedeutung. Beih. Bot. Centr., 45(1):50–73.

PONZO, A.

1929. La sinfillia nelle monocotiledoni. Nuovo Giorn. Bot. Ital., 36:203–241.

1932. Sulla filogenia delle monocotiledoni. Nuovo Giorn. Bot. Ital., 39:477–511.

POPE, MAXY A.

1925. Pollen morphology as an index to plant relationship. I. Morphology of pollen. Bot. Gaz., 80:63–73.

PORSCH, O.

1913. Die Abstammung der Monokotylen und die Blütennektarien. Ber. Deutsch. Bot. Ges., 31:580–590.

1931. Grellrot als Vogelblumenfarbe. Biol. Gen., 7:647–674.

1932. Die Vogelblume als Jagdköder des Blumenvogels. Biol. Gen., 8:271–282.

1933. Der Vogel als Blumenstäuber. Biol. Gen. 9(2):239–252.

1934–1935. Säugetiere als Blumenausbeuter und die Frage der Säugetierblume. I. Biol. Gen., 10:657–685; II, *Ibid.*, 11:171–188.

1937. Eine Nachtsäugetierblume mit fester Blütenlockspeise. Biol. Gen., 13:1–24.

1942. Eine neuer Typus Fledermausblumen. Biol. Gen., 15:283–294.

1950. Geschichtliche Lebenswertung der Kastanienblüte. Oesterr. Bot. Zeitschr., 97:269–321.

PRAT, H.

1932. L'épiderme des Graminées; étude anatomique et systématique. Ann. Sci. Nat., ser. 10, 14:117–324.

1936. La systématique des Graminées. Ann. Sci. Nat., ser. 10, 18:165–258.

PULLE, A.

1938. The classification of the spermatophytes. Chron. Bot., 4:109–113.

PURI, V.

1951. The role of floral anatomy in the solution of morphological problems. Bot. Rev., 17:471–553.

Puri, V. (Cont.)

1952a. Floral anatomy and inferior ovary. Phytomorphology, 2:122–129.

1952b. Placentation in angiosperms. Bot. Rev., 18:603–651.

1952c. Floral anatomy in relation to taxonomy. Agra Univ. Journ. Res., 1:15–35.

Rao, C. V.

1950. Pollen grains of Sterculiaceae. Journ. Indian Bot. Soc., 29:130–137.

1951. The vascular anatomy of flowers; a bibliography. Journ. Univ. Bombay, 19: 38–63.

1952. Floral anatomy of some Malvales and its bearing on the affinities of families included in the order. Journ. Indian Bot. Soc., 31:171–203.

Rao, H. S.

1939. Cuticular studies of Magnoliales. Proc. Indian Acad. Sci., 9(B):99–116.

Rao, T. A.

1951. Studies on foliar sclereids, a preliminary survey. Journ. Indian Bot. Soc., 30:28–39.

Rassner, Elfriede

1931. Primitive und abgeleitete Merkmale in Blütenbau einiger Ranunculaceen. Planta, 15:192–243.

Record, S. J.

1934. Role of wood anatomy in txaonomy. Trop. Woods, 37:1–9.

1936. Classification of various anatomical features of dicotyledonous woods. Trop. Woods, 47:12–27.

Record, S. J., and Margaret M. Chattaway

1939. List of anatomical features used in classifying dicotyledonous woods. Trop. Woods, 57:11–16.

Redfield, A. C.

1936. The distribution of physiological and chemical peculiarities in the "natural" groups of organisms. Amer. Nat., 70:110–122.

Reece, P. C.

1939. The floral anatomy of the avocado. Amer. Journ. Bot., 26:429–433.

Reeves, R. G.

1936. Comparative anatomy of the seeds of cottons and other Malvaceous plants. Amer. Journ. Bot., 23:291–296, 394–405.

Reichert, E. T.

1913. The Differentiation and Specificity of Starches in Relation to Genera, Species . . . Carnegie Inst. Wash. Publ. 173. xvi + xvi + 900 pp.

Rendle, A. B.

1903. The origin of the perianth in seed-plants. New Phytol., 2:66–72.

1904. The Classification of Flowering Plants. Vol. I. Gymnosperms and monocotyledons. xiv + 403 pp. Cambridge: Univ. Press.

1925. The Classification of Flowering Plants. Vol. II. Dicotyledons. xix + 636 pp. Cambridge: Univ. Press.

Rickett, H. W.

1944. The classification of inflorescences. Bot. Rev., 10:187–231.

Riek-Haussermann, Clara

1944. Vergleichend-anatomische und entwicklungsgeschichtliche Untersuchungen über Samen in der Gattung *Veronica*. Beith. Bot. Centr., 62A:1–60.

ROBERTSON, C.

1904. The structure of the flowers and the mode of pollination of the primitive angiosperms. Bot. Gaz., 37:294–298.

RODRÍGUEZ, R. L.

1950. A graphic representation of Bessey's taxonomic system. Madroño, 10:214–218.

1953. Systematic anatomical studies on *Myrrhidendron* and other woody Umbellales. (Thesis.) Univ. Calif.

ROEDERER, H.

1930. Die Phylogenie des Rosales-Astes. Bot. Archiv, 29:330–436.

ROLLINS, R. C.

1952. Taxonomy today and tomorrow. Rhodora, 54:1–19.

RUFF, O.

1931. Zur Phylogenie des Columniferen-Astes der Dikotylen. Bot. Archiv, 31:1–140.

SACHS, J. VON

1890. History of Botany (1530–1860). Transl. by H. E. F. Garnsey; rev. by I. B. Balfour. xv + 568 pp. Oxford: Clarendon Press.

SAHNI, B.

1932. *Homoxylon rajmahalense*, gen. et sp. nov., a fossil angiospermous wood, devoid of vessels, from the Rajmahal Hills, Bahar. Mem. Geol. Surv. India, Palaeont. Indica, 20(2):1–19.

1935. *Homoxylon* and related woods and the origin of the angiosperms. Proc. 6th Internat. Bot. Congr., Amsterdam, 2:237–238.

SALISBURY, E. J.

1926. Floral construction in the Helobiales. Ann. Bot., 40:419–445.

1942. The Reproductive Capacity of Plants; Studies in Quantitative Biology. xi + 244 pp. London: G. Bell & Sons.

SAMUELSSON, G.

1913. Studien über die Entwicklungsgeschichte der Blüten einiger Bicornes-Typen; ein Beitrag zur Kenntnis der systematischen Stellung der Diapensiaceen und Empetraceen. Svensk Bot. Tidskr., 7:97–188.

SARGANT, ETHEL

1902. The origin of the seed-leaf in monocotyledons. New Phytol., 1:107–113.

1903. A theory of the origin of monocotyledons, founded on the structure of their seedlings. Ann. Bot., 17:1–92.

1904. The evolution of monocotyledons. Bot. Gaz., 37:325–345.

1905. The early history of angiosperms. Bot. Gaz., 39:420–423.

1908. The reconstruction of a race of primitive angiosperms. Ann. Bot., 22:121–186.

SATINA, SOPHIE, and A. F. BLAKESLEE

1941. Periclinal chimeras in *Datura stramonium* in relation to development of leaf and flower. Amer. Journ. Bot., 28:862–871.

1943. Periclinal chimeras in *Datura* in relation to the development of the carpel. Amer. Journ. Bot., 30:453–462.

SAUNDERS, EDITH R.

1937. Floral Morphology; a New Outlook with Special Reference to the Interpretation of the Gynaeceum. Vol. I. viii + 132 pp. Cambridge: W. Heffer and Sons.

1939. Floral Morphology; a New Outlook with Special Reference to the Interpretation of the Gynaeceum. Vol. II. xiv + 477 pp. Cambridge: W. Heffer and Sons.

SAUNDERS, EDITH R. (Cont.)

1939. The neglect of anatomical evidence in the current solutions of problems in systematic botany. New Phytol., 38:203–209.

SAVILLE, D. B. O.

1953. Splash-cup dispersal mechanism in *Chrysosplenium* and *Mitella*. Science, 117: 250–251.

SCHAEPPI, H.

1936. Zur Morphologie der Gynoeceums der Phytolaccaceen. Flora, ser. 2, 31:40–59.

1939. Vergleichend-morphologische Untersuchungen an dem Staubblättern der Monocotyledonen. Nova Acta Leop.-Carol. (II), 6:389–447.

SCHAFFNER, J. H.

1934. Phylogenetic taxonomy of plants. Quart. Rev. Biol., 9:129–160.

1937. The fundamental nature of the flower. Bull. Torrey Club, 64:569–582.

SCHELLENBERG, G.

1928. Beiträge zu einen phylogenetischen System der Blütenpflanzen. Beibl. Viertalj. Naturf. Ges. Zürich, 73:355–381.

SCHNARF, K.

1931. Vergleichende Embryologie der Angiospermen. 354 pp. Berlin: Gebr. Borntraeger.

1933. Die Bedeutung der embryologischen Forschung für das natürliche System der Pflanzen. Biol. Gen., 9(2):271–288.

1936. Contemporary understanding of embryo-sac development among angiosperms. Bot. Rev., 2:565–600.

1937a. Studien über den Bau der Pollenkörner der Angiospermen. Planta, 27:450–465.

1937b. Ziele und Wege der vergleichenden Embryologie der Blütenpflanzen. Verh. Zool.-Bot. Ges. Wien, 86/87:140–147.

SCHÖFFEL, K.

1932. Untersuchungen über den Blütenbau der Ranunculaceen. Planta, 17:315–371.

SENN, H. A.

1938. Chromosome number relationships in the Leguminosae, Bibl. Genet., 12:175–336.

SINNOTT, E. W.

1914. Investigations on the phylogeny of the angiosperms. No. 1. The anatomy of the node as an aid in the classification of angiosperms. Amer. Journ. Bot., 1:303–322.

1916. The evolution of herbs. Science, Series 2, 44:291–298.

SINNOTT, E. W., and I. W. BAILEY

1914. Investigations on the phylogeny of the angiosperms. No. 4. The origin and dispersal of herbaceous angiosperms. Ann. Bot., 28:547–600.

1915a. Changes in the fruit types of angiosperms coincident with the development of the herbaceous habit. Science, Series 2, 41:179. (Abs.)

1915b. The evolution of herbaceous plants and its bearing on certain problems of geology and climatology. Journ. Geol., 23:289–306.

SMITH, G. H.

1926. Vascular anatomy of Ranalian flowers. I. Ranunculaceae. Bot. Gaz., 82:1–29.

SMITH, R. B.

1950. The role of mechanics in the evolution of the herbaceous plant stem. Bot. Gaz., 111:262–286.

Smith, W. W.

1936. Problems in classifications of plants. Journ. Roy. Hort. Soc., 61:77–90, 117–134.

Solereder, H.

1908. Systematic Anatomy of the Dicotyledons. Transl. by L. A. Boodle and F. E. Fritsch. 2 vols. Oxford: Clarendon Press.

Sporne, K. R.

1948. Correlation and classification in dicotyledons. Proc. Linn. Soc., 160:40–47.

1949. A new approach to the problem of the primitive flower. New Phytol., 48:259–276.

Sprague, T. A.

1925. The classification of dicotyledons. Journ. Bot., 63:9–13, 105–113.

1940. Taxonomic botany, with special reference to the angiosperms. *In* J. Huxley, New Systematics, pp. 435–454.

Sprotte, K.

1940. Untersuchungen über Wachtsum und Nervatur der Früchtblatter. Bot. Archiv, 40:463–506.

Staudermann, W.

1924. Die Haare der Monokotylen. Bot. Archiv, 8:105–184.

Stebbins, G. L.

1938. Cytological characteristics associated with the different growth habits in the dicotyledons. Amer. Journ. Bot., 25:189–198.

1950. Variation and Evolution in Plants. xix + 643 pp. New York: Columbia Univ. Press.

1951. Natural selection and the differentiation of angiosperm families. Evolution, 5:299–324.

Stern, W. L.

1952. The comparative anatomy of the xylem and the phylogeny of the Julianiaceae. Amer. Journ. Bot., 39:220–229.

Stoudt, H. N.

1941. The floral morphology of some of the Capparidaceae. Amer. Journ. Bot., 28: 664–675.

Suessenguth, K.

1921. Beiträge zur Frage des systematischen Anschlusses der Monokotylen. Beih. Bot. Centr., 38(2):1–79.

Suessenguth, K., and H. Merxmüller

1952. Ueber die Herkunft der Angiospermen. Phyton, 4:1–8.

Swamy, B. G. L.

1949. Further contributions to the morphology of the Degeneriaceae. Journ. Arnold Arbor., 30:10–38.

Swamy, B. G. L., and I. W. Bailey

1949. The morphology and relationships of *Cercidiphyllum*. Journ. Arnold Arbor., 30:187–210.

1950. *Sarcandra*, a vesselless genus of the Chloranthaceae. Journ. Arnold Arbor., 31:117–129.

Takhtajan, A. L.

1953. Phylogenetic principles of the system of higher plants. Bot. Rev., 19:1–45.

Taylor, F. H.

1939. Comparative anatomy of the secondary xylem in the Violaceae and Flacourtiaceae. Amer. Journ. Bot., 25:20s. (Abs.)

Tepfer, S. S.

1953. Floral anatomy and ontogeny in *Aquilegia formosa* var. *truncata* and *Ranunculus repens*. Univ. Calif. Publ. Bot., 25:513–648.

Thoday, D.

1939. The interpretation of plant structure. Advancem. Sci., 1:84–104.

Thomas, H. H.

1931. The early evolution of the angiosperms. Ann. Bot., 45:647–672.

1932. The old morphology and the new. Proc. Linn. Soc., 145:17–32.

1934. The nature and origin of the stigma; a contribution towards a new morphological interpretation of the angiosperm flower. New Phytol., 33:173–198.

1936. Paleobotany and the origin of the angiosperms. Bot. Rev., 2:397–418.

Thompson, J. M.

1935. The acarpous nature of modern flowering. Proc. 6th Internat. Bot. Congr. Amsterdam, 2:122–124.

1944. Towards a modern physiological interpretation of flowering. Proc. Linn. Soc., 156:46–68.

Thompson, W. P.

1918. Independent evolution of vessels in Gnetales and angiosperms. Bot. Gaz., 65:83–90.

1923. The relationships of the different types of angiospermic vessels. Ann. Bot., 37:183–192.

Thomson, Betty F.

1942. The floral morphology of the Caryophyllaceae. Amer. Journ. Bot., 29:333–349.

Tippo, O.

1938. Comparative anatomy of the Moraceae and their presumed allies. Bot. Gaz., 100:1–99.

1940. The comparative anatomy of the secondary xylem and the phylogeny of the Eucommiaceae. Amer. Journ. Bot., 27:832–838.

1946. The role of wood anatomy in phylogeny. Amer. Midl. Nat., 36:362–372.

Tischler, G.

1929. Verknüpfungsversuche von Zytologie und Systematik bei den Blütenpflanzen. Ber. Deutsch. Bot. Ges., 47:(30–(49).

Troll, W.

1927. Zur Frage nach der Herkunft der Blumenblätter. Flora, 122:57–75.

1928. Zur Auffassung des parakarpen Gynaeceums und des coenokarpen Gynaeceums überhaupt. Planta, 6:255–276.

1932. Morphologie der schildförmigen Blätter. Planta, 17:153–314.

1933a. Beiträge zur Morphologie des Gynaeceums. III. Ueber das Gynaeceum von *Nigella* und einiger anderer Helleboreen. Planta, 21:266–291.

1933b. Beiträge zur Morphologie der Gynaeceums. IV. Ueber das Gynaeceum der Nymphaeaceen. Planta, 21:447–485.

1934. Ueber Bau und Nervatur des Karpelle von *Ranunculus*. Ber. Deutsch. Bot. Ges., 52:214–220.

1939a. Ueber die morphologische Natur der Blütenorgane. Biologe, 9:39–44.

1939b. Die morphologische Natur der Karpelle. Chron. Bot., 5:38–41.

TUPPER, W. W.
1934. Preliminary report on the wood structure of the Flacourtiaceae. Trop. Woods, 38:11–14.

TURESSON, G.
1930. Genecological units and their classificatory value. Svensk Bot. Tidskr., 24: 511–518.

TURRILL, W. B.
1936. Contacts between plant classification and experimental botany. Nature, 137: 563–566.
1938. The expansion of taxonomy with special reference to Spermatophyta. Biol. Rev. 13:342–373.
1942. Taxonomy and phylogeny. Bot. Rev., 8:247–270, 473–532, 655–707.

TUTIN, T. G.
1952. Phylogeny of flowering plants: fact or fiction? Nature, 169:126–127.

TUZSON, J. VON
1936. Beiträge zur Entwicklungsgeschichte der Monokotylen. Proc. 6th Internat. Bot. Congr. Amsterdam, 1:324–329.

UNRUH, M.
1939. Die morphologische Bedeutung des Karpells. Beitr. Biol. Pflanz., 26:90–124.

VEH, R. VON
1930. Untersuchungen und Betrachtungen zum Blattstellungsproblem. Flora, 125: 83–154.

VENKATESWARLU, J.
1952. Embryological studies in Lecythidaceaes. I. Journ. Indian Bot. Soc., 31:103–116.

VESTAL, P. A.
1937. The significance of comparative anatomy in establishing the relationship of the Hypericaceae to the Guttiferae and their allies. Philip. Journ. Sci., 64: 199–256.
1940. Wood anatomy as an aid to classification and phylogeny. Chron. Bot., 6:53–54.

VUILLEMIN, P.
1919. L'amphigonelle et la phylogénie des Amentales. Ann. Sci. Nat., ser. 10, 1:139–200.

WAHL, H. A.
1940. Chromosome numbers and meiosis in the genus *Carex*. Amer. Journ. Bot., 27: 458–470.

WALTON, J.
1952. L'évolution des téguments et de la protection du sporange. Ann. Biol. III, 56:C. 129–C. 132.

WATSON, E. V.
1943. The dynamic approach to plant structure and its relation to modern taxonomic botany. Biol. Rev., 18:65–77.

WEBBER, IRMA E.
1934. Systematic anatomy of the woods of the Malvaceae. Trop. Woods, 38:15–36.
1936. Systematic anatomy of the woods of the Simarubaceae. Amer. Journ. Bot., 23:577–587.
1941. Systematic anatomy of the woods of the Burseraceae. Lilloa, 6:441–465.

WEEVERS, T.

1933. Die Pflanzenalkaloids, phytochemisch und physiologisch betrachtet. Rec. Trav. Bot. Néerl., 30:336–463.

1943. The relation between taxonomy and chemistry of plants. Blumea, 5:412–422.

WERNHAM, H. F.

1911–1912. Floral evolution; with particular reference to the sympetalous dicotyledons. New Phytol., 10:74–83, 109–120, 145–159, 217–226, 293–305; 11:145–166, 217–235, 290–305, 373–397.

WERMUND, R.

1928. Untersuchungen über die Brauchbarkeit der Serodiagnostik für die botanische Verwandtschaftsforschung, mit besonderer Berücksichtigung der Reihe der Rhoeadales, sowohl unter Anwendung der Präzipitationsmethode, als auch der Konglutinationsmethode nach Mez. Beitr. Biol. Pflanz., 16:39–80.

WERTH, E.

1923. Ueber die Bestaubung von *Viscum* und *Loranthus* und die Frage der primivität der Windblütigkeit wie der Pollenblumen bei den Angiosperm. Ber. Deutsch. Bot. Ges., 41:151–164.

1941. Die Blütennektarien der Ranunculaceen und ihre phylogenetische Bedeutung. Ber. Deutsch. Bot. Ges., 59:246–256.

WETMORE, R.

1926. Organization and significance of lenticels in dicotyledons. Bot. Gaz., 82:71–88, 113–131.

WETTSTEIN, R.

1924. Handbuch der systematischen Botanik. 3rd ed. viii + 1017 pp. Leipzig and Vienna: F. Deuticke.

WHITAKER, T. W.

1933. Chromosome number and relationship in the Magnoliales. Journ. Arnold Arbor., 14:376–385.

1934. Chromosome constitution in certain monocotyledons. Journ. Arnold Arbor., 15:135–143.

WHITEHOUSE, H. L. K.

1950. Multiple-allelomorph incompatibility of pollen and style in the evolution of the angiosperms. Ann. Bot., n.s., 14:199–216.

WIELAND, G. R.

1929. Antiquity of the angiosperms. Proc. Internat. Congr. Plant Sci. Ithaca, 1:429–456.

1931. Why the angiosperms are old. Science, 74:219–221.

1933. Origin of angiosperms. Nature, 131:360–361.

1934. Wood anatomy and angiosperm origin. Trop. Woods, 39:1–11.

WILKINSON, ANTOINETTE M.

1949. Floral anatomy and morphology of *Triosteum* and of the Caprifoliaceae in general. Amer. Journ. Bot., 36:481–489.

WILKINSON, J.

1944. The cytology of *Salix* in relation to taxonomy. Ann. Bot., n.s., 8:269–284.

WILSON, C. L.

1937. The phylogeny of the stamen. Amer. Journ. Bot., 24:686–699.

1941. The evolution of the stamen. Chron. Bot., 6:245.

Wilson, C. L. (Cont.)

1942. The telome theory and the origin of the stamen. Amer. Journ. Bot., 29:759–764.

1950. Vasculation of the stamen in the Melastomaceae, with some phyletic implications. Amer. Journ. Bot., 37:431–444.

Wilson, C. L., and T. Just

1939. The morphology of the flower. Bot. Rev., 5:97–131.

Winkler, H.

1931. Die Monokotylen sind monokotyl. Beitr. Biol. Pflanz., 19:19–34.

1936a. Habitus und Phylogenie. Beitr. Biol. Pflanz., 24:1–11.

1936b. Septizide Kapsel und Spaltfrucht. Beitr. Biol. Pflanz., 24:191–200.

1939. Versuch eines "natürlichen" Systems der Früchte. Beitr. Biol. Pflanz., 26: 201–220.

1940. Zur Einigung und Weiterführung in der Frage des Fruchtsystems. Beitr. Biol. Pflanz, 27:92–130.

1941. Verstehen wir das Gynözeum der Angiospermen schon? Beitr. Biol. Pflanz., 27:242–267.

Withner, C. L.

1941. Stem anatomy and phylogeny of the Rhoipteleaceae. Amer. Journ. Bot., 28: 872–878.

Wodehouse, R. P.

1928. The phylogenetic value of pollen characters. Ann. Bot., 42:891–934.

1931. Pollen grains in the identification and classification of plants. VI. Polygonaceae. Amer. Journ. Bot., 18:749–764.

1935. Pollen Grains; Their Structure, Identification and Significance in Science and Medicine. xv + 574 pp. New York: McGraw-Hill.

1936a. Evolution of pollen grains. Bot. Rev., 2:67–84.

1936b. Pollen grains in the identification and classification of plants. VIII. The Alismataceae. Amer. Journ. Bot., 23:535–539.

Woodson, R. E.

1935. Observations on the inflorescence of Apocynaceae. Ann. Mo. Bot. Gard., 22:1–48.

Woodson, R. E., and J. A. Moore

1938. The vascular anatomy and comparative morphology of Apocynaceous flowers. Bull. Torrey Club, 65:135–166.

Worsdell, W. C.

1903. The origin of the perianth of flowers. New Phytol., 2:42–48.

1907. The origin of the "flower." Sci. Progr., 2:255–262.

1908. A study of the vascular system in certain orders of the Ranales. Ann. Bot., 22:651–682.

Worseck, E.

1922. Sero-diagnostiche Untersuchungen über die Verwandtschaftsverhältnisse der Monocotyledonen. Bot. Archiv, 2:177–206.

Wulff, H. D.

1939. Die Pollenentwicklung der Juncaceen nebst einer Auswertung der embryologischen Befunde hinsichtlich einer Verwandtschaft zwischen den Juncaceen und Cyperaceen. Jahrb. Wiss. Bot., 87:533–556.

Wunderlich, Rosalie

1936. Vergleichende Untersuchungen von Pollenkörnern einiger Liliaceen und Amaryllidaceen. Oesterr. Bot. Zeitschr., 85:30–55.

Wunderlich, Rosalie (Cont.)

1950. Die Agavaceae Hutchinsons im Lichte ihres Embryologie, ihres Gynözeums-, Staubblatt- und Blattbaues. Oesterr. Bot. Zeitschr., 97:438–502.

Ziegenspeck, H.

1938. Die Phylogenie der Glumiflorae. Bot. Archiv, 39:177–205.

Zimmermann, G. Z.

1932. Ueber die extrafloralen Nektarien der Angiospermen. Beih. Bot. Centr., 49(1): 99–196.

Zimmermann, W.

1930. Die Phylogenie der Pflanzen; ein Ueberblick über Tatsachen und Probleme. xi + 452 pp. Jena: G. Fischer.

1935. Die Phylogenie der Angiospermen-Blütenstände. Beih. Bot. Centr., 53A(1): 95–121.

Zinke, W.

1924. Ueber das Assimilationsgewebe der Monokotylen und seine Verwendung in der Frage ihres systematischen Anschlusses. Bot. Archiv, 5:74–91.

Zohary, M.

1950. Evolutionary trends in the fruiting head of Compositae. Evolution, 4:103–109.

SYSTEMATIC ENTOMOLOGY

By EDWARD S. ROSS
California Academy of Sciences
AND
COLLABORATORS

INTRODUCTION

By EDWARD S. ROSS
California Academy of Sciences

Like a group of artists painting a large mural, workers in science should periodically pause in their labors and survey what has already been accomplished. Such a general inspection would benefit the whole project, enabling each participant to return to his individual section with a better idea of how he may contribute to the completion of the "big picture." The "canvas" of entomology is the most extensive of all the natural sciences. Although the picture is sketchy in places and far from complete, so much work has been done, especially in the last half of the century under consideration, that it is difficult for one person to see it all. The study of an order, or even of a family, of insects may be more extensive, and perhaps more important, than some entire branches of science to which greater space is devoted in this volume.

In order to provide material of real use as reference I have asked various specialists to evaluate the accomplishments of the past century in the particular sections of entomology with which they deal. An attempt has been made to treat all the orders in these reports and, although there are gaps, the coverage is sufficiently complete to allow some generalizations concerning progress and trends. I am deeply greateful to each contributor for his cooperation.

Although it is not the purpose of these papers to introduce new systematic concepts, an exception is made for Dr. Remington's review of the Apterygota. The modification of insect classification which he includes in his historical review of apterygotan studies is sufficiently interesting to warrant the use of additional space.

As my own contribution I would like to offer some general observations on the present state of insect systematics from the point of view of a curator of a large insect collection. An evaluation of the past efforts in systematic entomology as a means of understanding the needs of the future seems preferable to a chronological review of events in this Century of Progress.

The evidence of progress in any period of systematics is published names, descriptions, illustrations, and keys, together with preserved specimens. The century 1853–1953 produced a quantity of each of these in entomology—more, in fact, than in other branches of natural science. Much of this is something to be proud of, but as we examine the accumulations closely, we find that a large part of this past effort constitutes a burden to future progress. The attempt to discover exactly what a given author was trying to name often takes time that the skilled worker could otherwise use for advances in our real knowledge. Theoretically, at least, the solution of such problems of nomenclature is simple. All one has to do is to examine each holotype specimen and interpret correctly the name it represents. In practice, however, this is very difficult, if not impossible, especially for names proposed before the holotype concept was established. Ironically, the more puzzling and inadequate the author's published work, the more important are his preserved specimens.

We all look to the museum to preserve the collections that form the basis of all nomenclature. Here, however, we find a poorly supported activity, for it is hard to justify the need for support in the eyes of those who have never themselves tried to solve the problems for which the museum alone provides the clues. Also, the scattered distribution of types among institutions and private collections sets up obstacles. All too often type specimens are considered in relation to the prestige of the collections possessing them rather than in relation to their service to science. Let us hope that some day types will be concentrated in fewer places.

The abundance of insect species and their tremendous biological diversity, evolved over a great span of geological time, should provide ideal materials for developing broad biological principles. This very abundance, however, is the root of our difficulties in nomenclature. The common mistake of many entomologists is the distribution of their efforts over too broad a taxonomic field, with the result that their classifications are often based on very superficial knowledge. A modern student has first to extricate himself from the maze of faulty nomenclature before he can see the objects of his specialty as living creatures. All too often he becomes involved with—and even absorbed in—the puzzles of the literature, priority, and so on. As a matter of fact, pure entomology is unique among the biological sciences in being dominantly systematic, a fact which indicates the appropriateness of including in this volume a paper in this field.

In this discussion I do not wish to imply that *all* papers that consist merely of descriptions, keys, and illustrations are to be regarded as works inferior to those in other branches of science. Every stage or conclusion in such standard taxonomic papers may reflect—indeed should reflect—judgments that draw upon the broadest type of experience of a research biologist. No science should be wholly condemned because it is poorly practiced by some.

The establishment of a sound classification, however, is only one aspect of our research in entomology. It should not become a specialist's all-absorbing purpose, else the very classification he seeks to establish may prove faulty. The modern approach to a field of study is necessarily through specialization, which makes advanced investigation possible.

Unfortunately the nature of insects, their abundance, beauty, convenient size, ease of preservation, and the way in which specimens can be lined up in neat attractive rows have long caused them to be "collectors' items." Many of the authors of earlier taxonomic literature were, in effect, collectors who just happened to limit their objectives and technique to insects. Many of them often had no desire to be biologists. Thomas L. Casey, who described about 9,400 species of Coleoptera, mostly from the United States, is an excellent example of this type of worker. Such workers may at times write skillful detailed descriptions of the external features of a limited series of long dead, partially examined specimens, but they seldom have a knowledge of the species as living elements. Few of them investigate the basic anatomy of their subjects, the biology and developmental stages, or the full geographic distribution of genera in order to assemble data leading to a sound and lasting classification.

Thus the lamentable tendency in entomology is not to specialize in a broad zoological sense in the study of a limited group of organisms. There is instead a marked tendency to study only one aspect or phase of a large group—often that of an extensive order. Thus we have not only taxonomists but specialists within taxonomy, i.e., species describers, cataloguers, specialists in nomenclatural law, and so on. Sometimes, particularly to serve the needs of applied entomology, certain specialists will study just the larval stage of a group; while others study the adults, with little or no knowledge of the larvae. Other specialists may study the group's biology, and still others its anatomy and physiology, or its importance in applied science.

There are many good reasons why this has happened, most of which involve individual aptitude, training, ability, or desire. Behind all this lies the factor of the size of the insect world. An almost limitless supply of raw material is available to stimulate the production of the superficial taxonomist. Furthermore, in any generation the workers studying a given group may be so few, and they may have so much in common, that criticism is absent.

It thus seems to me that the greatest step toward the improvement of future systematic studies would be for each worker to deal intensively with a special taxonomic group, a group sufficiently limited so that he will not be required to adopt arbitrary and artificial geographic bounds. It will then be possible for him actually to know the literature, and there would be real hope for a sound evaluation of the past nomenclature, based, as far as possible, on the examination of types. Progress in this phase might be marked by the publication of revisionary works of lasting value. Once the taxonomic situation is in hand, a worker, instead of passing on to the systematics of some other group (as he will undoubtedly do, regardless of this discussion), should initiate or accelerate truly biological investigations of the group. Novelties in the unstudied material in museums can then be described with a clear conscience. Field trips can be made, when necessary, to regions where the specimen sampling is incomplete or is promising. Whatever the region, new discoveries will fall into proper order, often indicating new concepts for examination. Biological, anatomical, and other lines of inquiry can be reported upon and used as data for perfecting systematics, and all information can be "card indexed," with an increasingly sound and stabilized nomenclature.

Many will argue that, if all the workers of the past had been engaged in investigations of this intensive type, conducting broad studies within small sections of the insect world, we would today have a very uneven coverage of the field. Certain groups would be known in great detail, others very poorly. The insect world would not be "blocked out" as well as it now is. One could debate this point at length. The question remains, however, whether entomology might not have contributed more toward our modern concepts of evolution, genetics, and zoogeography, if more penetrating detailed studies had been made in place of the skimmings in systematics that characterize the past. Certainly it is doubtful whether, if other animal groups were as rich in species as the insects, biological science could have attained its present level. Indeed, many of the present concepts of enlightened entomological systematists have developed from the study of birds, mammals, and other small groups, whose systematics matured more rapidly.

The most fortunate modern systematists are those who study the unpopular, difficult-to-handle insect groups that have been largely ignored in the past. Here, in both literature and nomenclature the slate is relatively clean and one can almost at once apply modern techniques and adopt new points of view. This advantage applies particularly to insects that require special preparation on microscope slides. Here, in the past, inadequate preparations have been responsible for some very bad work, but when a student has used proper techniques he is often rewarded by a wonderful array of useful details, and his work tends to be sound.

It is always easy, however, to look at the past and comment on how things should have been done. In order to understand why things happened as they did in systematic entomology, let us briefly summarize the historical development of our science.

Beginnings in Europe

Quite logically, systematic entomology began in northwestern Europe. Here the relative freedom from control by Church and State and the expanding communication through printed material were the incentives for increased intellectual expression in science as well as in other branches of human endeavor. Here also, wealth from growing industry, trade, and colonialism freed many individuals from a life completely devoted to mere existence. There was time for contemplating the nature of things about one, for the satisfaction of curiosity for curiosity's sake.

To write or talk about things, things must be named. Linnaeus' binomial system of nomenclature started the great rush to name and classify all of the living things in Europe as well as the strange exotic creatures brought home by travelers.

Insects provided, and still provide, the most fruitful field for this endeavor. With the prevailing belief in special creation and the relative simplicity of the fauna in northwestern Europe, the early Linnean disciples must have had little idea of the magnitude and complexity of the task which they began. With our present knowledge, even the most ardent modern "species grinder" would derive little satisfaction from the prospect of plodding along on so vast a project with so small an audience.

The early systematists had one great advantage, however evanescent—a very limited literature and nomenclature. Furthermore, they lived among the creatures they described. If written descriptions were poor, they could practically go out into the surrounding countryside and, by a process of elimination, discover what their fellow worker had tried to describe. Nevertheless, nomenclatural dilemmas set up by these pioneers remain to this day the most difficult problems with which we have to contend.

Another advantage, closely linked with the preceding, was peculiar to Europe. Each worker belonged to a relatively settled, culturally distinct population, occupying a limited geographic area. Each country was like a snug island; Great Britain, from which perhaps the greatest per capita number of systematic studies have appeared, was literally so. As a result, each country began to develop its own group of enthusiastic amateur entomologists. There was a real stimulus for these beginners in the fact that their collecting was confined within definite geographic bounds. There was an excellent chance to secure in one's lifetime a nearly complete collection of at least the larger insects; the nearer to completion the collection, the more exciting the hobby.

Many regional treatments appeared, which attracted and aided new workers, and each manual or catalogue played an important part in refining and perfecting the knowledge of the local fauna. Some workers were collectors only, but their special enthusiasm increased the number of specimens available to more advanced workers. By 1853 many of the more popular insect groups in Europe —especially the larger Lepidoptera and the Coleoptera—were almost completely sampled and named. Hatch (p. 556) illustrates this point by showing that 3,650 species of beetles occurring in Britain had been named by 1832. By 1945 this number had increased by only 61 names! Of course there were actually more novelties than this in the 121 years, because of synonyms in the 1843 list, but these figures testify to the thoroughness and enthusiasm of a group of naturalists working within definite geographic bounds. Fortunately there was pretty good coordination of nomenclature from country to country, and excellent Pan-European treatments developed from the national studies. The most important result of this regional activity was that the local manuals provided a fertile field for the development of beginners. At any time the size of the mature crop of advanced scientists is proportional to the number of seeds that are sown and sprout. Popular regional works nourish the growth of "seedling" scientists, some of whom contribute only collections and their support to science, while others progress to broader scientific horizons.

Some of the early European amateurs, having seen the supply of local novelties reduced, turned their attention more and more to the foreign field. Much of their work appeared as special reports of expeditions or in regional monographs like the Biologia Centrali-Americana.

Many specialists in taxonomic rather than geographic units soon appeared on the European scene and began the type of comprehensive research in special groups that is so vitally needed today. But, as is the rule among entomologists, they still persisted, even at the superficial taxonomic level, in attempting more than they could properly accomplish.

Because of all this amateur activity several entomological societies and periodicals were founded in Europe well before 1853, and the number has steadily increased. At first there was objection to specialization and even today there remain important vestiges of the old general philosophical organizations and periodicals. (The *Proceedings* of this Academy is an example.) Although such periodicals tend to scatter the literature of a subject, they do provide outlets for publication in fields that are unable to support their own journals. At present there are even a number of periodicals that deal only with insects of a single order, like the Coleoptera and Lepidoptera. It is interesting to speculate on the possibility that at some future time at least the small papers and notes concerning each major insect group will appear in their own specialized publications.

Thus Europe became the fatherland or heartland of systematic entomology. Ideally, each specialist, regardless of his location, should begin his studies with the European fauna, especially the type species of European genera, before proceeding to study the fauna of any other region. Much confusion in nomenclature is due to erroneous assignments of foreign species to European genera or to a failure to assign new species to the known European genera. This is particularly true, of course, in other north-temperature regions of the world.

Developments in America

When we turn our attention to America, the other great center of science and systematic entomology, we find the course of events quite different. Like all pioneers, the early colonists in America were far too busy creating a new society in the wilderness to give much time to the study of fauna and flora, unless these proved edible. Some cynics will say that the same attitude prevails in America to this day, and there is some truth in this; in many ways we are still unsettled nations, experiencing great population shifts.

To the need for justifying an activity as serving some practical end, was added the fact that most of the emigrants in those days were people who were least likely to have been well enough established at home before their departure from Europe to engage in a scientific hobby.

Some American insects did reach the hands of European workers, but not until the time of Thomas Say did important systematic studies in America begin. As Hatch, in the Coleoptera section of this series, points out, the scope of systematic studies did not long remain confined to the New England states where they began. Almost at once portions of the population moved westward and, augmented by a steady stream of unsettled European emigrants, rapidly formed bustling, almost Continental nations. Even today the number of Americans who have studied insects has been woefully inadequate to cope effectively with the rich insect fauna awaiting description and classification. The task was magnified by the development of a regionalism that is particularly detrimental; the extent of which has made almost impossible the production of adequate popular treatments, which are needed to inspire the beginner and hold his interest until he is able to continue his work in the face of the difficulties and labor that confront anyone attempting serious advanced work.

Other influences besides geographic expanse soon affected the progress of systematic entomology. The Industrial Revolution of the past century caused great concentrations of urban populations, which became dependent on an intensive type of agricultural production for their food, while at the same time, the machines of the Revolution provided the tools the farmer needed for production on a vast scale. The transformation from diversified small-scale agriculture to specialized large-scale agriculture made more acute the attacks of insects. Some of these pests were native but, with increased and more rapid commerce, the introduction and intracontinental dissemination of pests from all parts of the world began, which resulted in a need for entomological service in agriculture. Soon, too, there developed an awareness of the medical importance of insects. Federal and State funds became available to economic entomology and, as the needs for entomological studies increased, so also did the staffs of teachers to train the required men. Thus there is today probably a greater corps of professionals in entomology than in any other branch of natural history.

All of this has had a marked effect on the progress of systematic entomology. Many men entered the field who had the advantage of broad training in science. Much purely scientific entomology was carried on as a side line by men whose official work was economic entomology or the training of economic entomologists. We owe a rather advanced knowledge of many insect groups to the fact that they include certain species of agricultural or medical importance; the fruit flies, bark beetles, fleas, and mosquitoes are but a few examples. Along with these advantages, however, there is an unfortunate tendency to evaluate entomological research in terms of its direct or foreseeable practical application.

Developments in Other Regions

Outside of Europe and North America a good deal of systematic work has been carried on in Japan, China, Indonesia, Australia, India, South Africa, Brazil, Argentina, and Chile. To a great extent in these countries faunas are studied chiefly by nonresident scientists. As a rule, a country or a state must enjoy a high standard of living for a long time before aesthetic science develops, that is, before knowledge can be sought solely for the love of knowledge. Many regions are handicapped by their inability to build up the required reference libraries and collections. Also, the fact that the type specimens of many of their native species are lodged in museums in far-off countries is a disadvantage. This circumstance, however, should not be used to justify an arbitrary ruling that types should be returned to the country of their origin, especially if safe and perpetual care of the specimens cannot be assured there. Types are best situated where the population of research workers is most dense.

Importance of the Amateur

I believe that the future of systematic entomology will be to a great extent dependent on the development of a large group of amateurs interested in insects. This does not necessarily mean that the amateur will do the basic scientific work himself, but the development by the general public of a definite interest in the science will create a "consumer demand" for the by-products of pure systematic studies, that is, for the manuals. This interest, too, will result in greater support for museums, for chairs of entomology in universities, and for scientific societies and publications.

Systematists today should therefore do everything they can to encourage more people to pursue the avocation of insect study or, at least, to appreciate such study and support facilities for it. Each large population center should be served by guidebooks of its local fauna so that the extent of the insect world may not appear overwhelming to the beginning amateur. This is particularly important in North America where a continent-wide fauna cannot be readily synopsized in a single work. Although obscure groups should be mentioned in their proper place in such manuals, major emphasis should be placed on the more conspicuous insects. A study of these becomes, in effect, an elementary classroom from which amateurs can graduate to the study of groups requiring more work. Amateurs, if they annotate their specimens fully, can at least accumulate data for the scientist to interpret. In many regions, for example, butterfly studies have advanced to a stage which involves the methods of a geneticist. But one of the main purposes of butterfly collecting can be to hold the interest of the beginner until he can perceive the deeper values of his pursuit, when he can apply his zeal to some lesser known section of the insect world.

The common complaint of specialists is that our knowledge is too incomplete or too tentative to produce synoptic works, but the reason for its incompleteness is the very lack of the workers whom the guidebooks would stimulate! The user of such manuals soon comes to appreciate the author's problems. Perhaps the book's deficiencies may stimulate the reader to become part of a team that will make possible more adequate work in the future. Out of every hundred amateurs, one or more may be impelled to take up some neglected phase of insect study and, with the guidance of advanced workers, pursue this study at its highest level.

The reason I have emphasized the role of the amateur is because it is the amateur who chiefly pioneered our science and because he holds the key to its future development. Even today the professional scientists who are motivated by the enthusiasm of the amateur make the greatest contributions to science. They are not mere nine-to-five-o'clock scholars; their studies are one of their main interests in life. As much as possible of their spare time, vacations, years of retirement, and financial resources is given to their work.

Such individuals are rare in any society because they work for things above and beyond their basic material needs. Unfortunately, their number does not seem to increase in proportion to the expanding opportunities afforded by our modern way of life. Indeed, highly advertised, commonplace, nonconstructive spare-time activities—or inactivities, like television—are capturing the time and mind of youth to a degree that may make the future crop of amateur scientists very scanty. If entomological studies are to rival these diversions, they must be made more available and more attractive.

Improvements in Systematic Method

Once a worker restricts his research to a field that he can actually handle, he can take the time to improve his methods, and his contributions will become more valuable and rewarding. Many will argue that specialization of this sort is undesirable, that a worker is apt to become narrow. I disagree; the more concentrated the field of study, the sooner the worker ceases to be a mere taxonomist. With concentration on a specialty, knowledge of what has been learned in related fields of science becomes more essential. The worker must know more and more about such subjects as climate, phytogeography, geology, paleontology and anatomy in order to evaluate the ideas that develop in the course of a penetrating investigation. Acquaintance with the conclusions of fellow workers conducting parallel studies in other insect groups likewise becomes increasingly important.

It is to be hoped that those individuals who devote themselves to such long-term, if not lifetime, specialization with no geographic boundaries or limitations on research will have come to this through a period of general entomological study. Often this general training affords a broad knowledge of the insects of some particular region, which can be drawn upon to aid beginners. The temptation to contribute isolated systematic studies of groups outside one's specialty should be avoided.

It should go without saying that one of the first objectives of a specialist is to examine thoroughly the creatures he studies. Strangely, many fail to do this. They seem rather to be satisfied with the reshuffling of old and new species on the basis of characters in vogue in the eighteenth or nineteenth centuries. An anatomical exploration should establish the homologies and terminology of parts, but it should also bring to light new, basic characters for determining relationships. Representative species of the group, especially type species of genera, should be chosen for this purpose. The generic classification should be well along before a worker becomes involved in problems of subspeciation. Once this comparative anatomical basis for classification is established, one can usually find superficial, easy-to-see features to use for key purposes.

While the systematic "truths" are being explored we should look for improved ways of telling others what we have seen. Fine line-drawings of critical anatomical parts are ideal for this purpose. Since these are the products of effort rather than talent, there is little excuse for their neglect. At least the pencil outlines should be made by the scientist himself, because the act of making drawings impels one to examine closely the things he studies. Anyone who feels that he cannot express himself in line-drawing should avoid systematic studies, since this is the best medium of communication in the field.

In publication, small isolated expositions of limited scope should be avoided unless the group has already been recently revised. Anyone who feels qualified to describe a new species should be able to present a revision of the genus involved, if it is needed.

The specialist, as he solves past nomenclature problems, should study his subjects in the field, and field trips for this purpose should be made as necessary. It has been my observation that a specialist can often accumulate more data during one short trip to an area than would have been possible in hundreds of years of general collecting by nonspecialists.

With a library of reprints and microfilm built up around a specialty a worker can become almost independent of large libraries and sets of periodicals. In a few years his specialized collection, except for types, may well become the best in existence. His time should not be taken up with the collecting and preservation of specimens in which he has no personal research interest. His books and specimens may later prove a most valuable legacy to his successors in the research field.

One of the greatest contributions toward the stabilizing of insect nomenclature, aside from the development of the international rules for zoological nomenclature, was the recognition of the importance of basing a name on a holotype specimen. There is still, however, considerable need for a greater understanding of the significance of the holotype. This is important, because such specimens, however arbitrarily selected, stand as the least subjective "anchor points" for all nomenclature. Unfortunately there are yet workers who confuse describing the holotype with describing the species (a never ending task). This confusion is also reflected in the designation of paratypes, which are often used as a means of exhibiting the *nature of the species* (i.e., characters of the opposite sex or castes; developmental stages; products, such as galls; and characters of other populations, by the introduction of individuals from other localities in the paratype series) rather than the *nature of the holotype*. As soon as this point is understood, the format of species description and paratype designation of many workers will need to be modified.

Entomologists in particular should realize that there will have to be some, perhaps arbitrary, point at which certain kinds of animal populations will cease to be designated by names that enter into zoological nomenclature. The only really definable unit in biology is the individual. If we continue the present trend of naming each apparently distinct population of individuals, we will develop a nomenclatural snarl that will defeat progress.

As a certain stability of nomenclature is reached in a group, research emphasis should be changed from the defining and naming of micropopulations to other forms of biological investigation. This shift of emphasis may indeed be used as a means of stabilization; at least, such aspects should be investigated by the systematist. I know of some insect groups in which detailed taxonomic work continues but of which not a single life-history study has ever been made. Here, of course, we encounter the age-old human equation—the type of mind to which taxonomy is appealing is often not attracted to any other phase of study. I sometimes think, too, that the collecting and classifying instincts in man are more basic and common than any other manifestations of his scientific curiosity. Certainly, because of the abundance and "convenient" nature of insects their study has attracted many persons dominated by these instincts.

Summary

1. Systematic studies have dominated, and yet at times have delayed, the development of biological research in entomology.

2. There is a need for broader specialization in more limited taxonomic units. This will tend to eliminate the pitfalls of research limited by geographic scope or life-history stage. More entomologists should be biologists studying a group of animals, not merely taxonomists studying the group.

3. The study of the insect world is too vast and mostly of too little economic importance, to be adequately carried on by specialists paid from public funds. More financial support will have to come from private funds and from the contributions of skilled amateur researchers.

4. The results of first-line systematic studies should be made available to the public in the form of popular works. These must be in sufficiently small regional "dosages" not to overwhelm the prospective user or, indeed, the compiler.

5. Aided and stimulated by such works, a larger corps of amateurs should develop to support the institutions and periodicals featuring purely scientific

entomology. The larger the group of beginners, the greater will be the number of skilled amateurs to aid the professional and his institutions.

6. In this next century, stress should be laid on quality of systematic production rather than on quantity. The organisms in each group should be more closely examined in search for better characters. Better methods of making expositions of the nature of old and new species must be investigated.

THE "APTERYGOTA"

Charles L. Remington
Osborn Zoological Laboratory, Yale University

The primitively wingless hexapods of the insect-myriapod line of evolution are still generally combined in what now appears to be a diverse and probably unnatural assemblage. Studies of their biology and systematics have lagged far behind such investigations of perhaps every other major group of the insects and their relatives. Essentially the entire published record of our knowledge of these "Apterygota" has appeared since the California Academy of Sciences was founded, a century ago. At that time the Protura were unknown. The first species of the Entotrophi had been recently described by Westwood. Not one important paper dealing solely with Thysanura (*s. str.*) had been published, although over forty species' names had been proposed by Linnaeus (from De Geer), Fabricius, Nicolet, Savigny, Lucas, Burmeister, and others, with largely useless descriptions. The Collembola were better known, through the substantial works of De Geer, Templeton, Bourlet, Gervais, Nicolet, and Lucas. Nicolet had described the internal and external morphology of Collembola, with many errors.

Phylogenetic Relationships of "Apterygota"

In 1853 all known "Apterygota" were usually grouped in a single order under Latreille's name, Thysanura. Latreille had earlier placed the Thysanura (*s. lat.*) with the Crustacea or with the Arachnida, but eventually (1825) he included only the hexapods in the Insecta, which were arranged as follows:

- Class Insecta
  - Section Aptera
    - Order Thysanoura
      - Family Lepismenae
      - Family Podurellae
    - Order Parasita (parasitic lice)
    - Order Siphonaptera
  - Section Alata

Burmeister, in his great *Handbuch der Entomologie* (1838), had lumped all the "neuropterous" and orthopterous insects in an order Gymnognatha, with ten *zünfte,* of which the third was Thysanura with the families Poduridae and Lepismatidae. In England and America a century ago the system probably used by entomologists was that of Westwood's *Entomologist's Text-book* (1838), with the following arrangement:

Insecta
    Class Crustacea
    Class Arachnida
    Class Ametabola
        Order Chilognatha (=Diplopoda)
        Order Chilopoda
        Order Thysanura
            Family Lepismidae
            Family Poduridae
        Order Anoplura
    Class Ptilota (winged orders and fleas)

By 1865 both *Campodea* and *Iapyx* were known, and Meinert combined them as the family Campodeae. He restricted the order Thysanura to that family and the family Podurae. The family Lepismae (= modern Thysanura) he grouped with the Orthoptera in another order under Fabricius' name, Ulonata. He recognized the affinity between the lepismatids and the Orthoptera, a closeness not shared with *Iapyx* and *Campodea*. We are now returning to such a view, although most of our reasons are not those of Meinert.

Lubbock (1870) first set aside the order Collembola as distinct. He referred to it as an "island" apart from the "continent" of true insects, including the Thysanura (*s. lat.*).

Packard was the earliest serious student of the American Collembola, Thysanura, and allied myriapod groups, and his contributions to their taxonomy and phylogeny are outstanding. He recognized the closeness of the remarkable Symphyla to the Collembola and the Cinura (= modern Entotrophi and Thysanura). Packard (1883) divided the insects into five superorders, four containing the groups with wings or with winged ancestors and the last as follows:

Superorder Synaptera
    Order Thysanura
        Suborder Cinura
        Suborder Symphyla
        Suborder Collembola

In the *Textbook* (1898) Packard later made the Synaptera one of two subclasses. The other combined the first four of his former superorders under Gegenbaur's (1878, p. 244) name Pterygota.

The separation of the "Campodeae" from the "Lepismae" by Meinert was generally ignored, but twenty-three years later Grassi (1888) presented a comprehensive monograph of the external and internal structures of these two groups, showing conclusively their distinctness. He proposed for the first time a higher category name for the *Campodea* and *Iapyx* group. Like Meinert, Grassi recognized the nearness of the Thysanura to the Orthoptera:

Superorder Orthoptera
    Order Thysanura
        Suborder Entotrophi
            Family Campodeadae
            Family Japygidae
        Suborder Ectotrophi
            Family Machilidae
            Family Lepismidae

Handlirsch (1903) followed Grassi's separation, but he elevated Grassi's suborders to the rank of classes, and the families became orders.

In 1901 Börner first divided the Collembola into two suborders, the elongate forms with relatively discrete abdominal segments being the Arthropleona and the globular forms with the abdominal segments much fused being the Symphypleona.

During the first quarter of the present century Handlirsch, Börner, and Crampton vied with each other in shuffling arrangements and names for the grouping of the primitively wingless hexapods, but little new evidence was produced or brought to bear on the problem.

The Protura were not recognized in print until 1907, when Silvestri described the first genus and species and placed them in a new order. While small, most Protura are easily seen with the naked eye. They occur abundantly in soil in all or nearly all temperate and tropical regions of the world. It is most curious that the Protura passed unnoticed for such a long time. Silvestri's exciting paper was followed soon by numerous others by several authors. In 1908 Berlese described the internal anatomy, and in 1909 he published a superb monograph of all aspects of the group. At that time, only two years after the order was named, he knew ten species.

Tillyard (1931) introduced a new theory of insect ancestry, in characteristically logical style. Stressing the site of the gonopore, which Packard had emphasized long before, Tillyard first divided the insects and close allies into two great groups, the Progoneata (Symphyla, Pauropoda, Diplopoda) and the Opisthogoneata (Chilopoda and hexapods). The hexapod line produced the Collembola, then Protura, then in successive steps the Projapygidae, Campodeidae, and the first "Ectotrophica." The last gave rise to two surviving lines, the Machilidae and the Lepismatidae, with the latter producing the Pterygota. Imms (1936, 1939, 1947) convincingly discounted the gonopore character and reasserted the old view that the Symphyla and Entotrophi (for which he used Börner's name, Diplura) are very closely related.

In 1940, in the first of a series of brilliant contributions, Tiegs showed that the gonopore of the Symphyla is not primarily anterior. He wrote: "The first instar larva presents the appearance of a potentially opisthogoneate myriapod. The secondary genital opening on the fourth segment develops in a later instar." He showed (1947) that the Pauropoda have a similar, but not necessarily monophyletic, secondary development of the cephalad gonoducts. Tiegs investigated the ontogenetic development of one or a few members each, of Symphyla (1940, 1945), Pauropoda (1947), Collembola (1942a), and Entotrophi (1942b) in more or less detail. He discovered in eggs of Symphyla, Collembola, and Entotrophi a remarkable "dorsal organ" which produces a cagelike net of long tendrils growing out around the embryo. Such an organ is not known in Thysanura, the Pterygota, or any other arthropod. Its complexity and yet striking similarity among the three groups having it suggest strongly a common ancestor not shared with other myriapods and a deep separation from the Thysanura and Pterygota, in both of which the amnion and serosa are present and may have displaced the "dorsal organ." I am proposing that this unique structure be called Tiegs' Organ in honor of the discoverer of its detailed nature and possible phylogenetic significance.

A review of the evidence now available leads one to the conclusion that the Pauropoda, Diplopoda, Chilopoda, Symphyla, Collembola, Protura, Entotrophi, Thysanura, and Pterygota are a series of forms with a common ancestor not shared with any other Arthropoda. Furthermore, the discontinuities between adjacent members of this series may seem large when one or two characters are considered, but always important linking characters complicate the establishment of classificatory groupings. The distribution of each of the characters believed to carry the most weight in phylogenetic reasoning can be summarized briefly.

1. *Cleavage:* Early cleavage is entire in the Pauropoda, Diplopoda, Chilopoda, Symphyla, and Collembola. It is incomplete in the Entotrophi, Thysanura, and Pterygota. The embryonic development of the Protura is unknown.

2. *Embryonic Membranes:* Amnion and serosa cover the entire embryo of Pterygota (rarely secondarily lost) and all but a small pore in the Thysanura. The Collembola, all four myriapod classes, and the Entotrophi lack these embryonic membranes.

3. *Tiegs' Organ:* This embryonic "dorsal organ" is absent in Pterygota, Thysanura, and Pauropoda and present in Collembola, Symphyla, and Entotrophi. The situation for embryos of Diplopoda and Chilopoda is not known.

4. *Embryonic Yolk-Cells:* Pauropoda, Diplopoda, and Symphyla have no segregation of vitellophags and tissue-forming cells. The other five groups whose embryonic development is known have separate vitellophages.

5. "*Pupoid Stage*": In the Pauropoda, Diplopoda, Chilopoda, and Collembola the embryo emerges precociously and undergoes an inactive phase within the embryonic cuticle. This stage does not exist in Symphyla, Entotrophi, Thysanura, or Pterygota.

6. *Anamorphosis:* Pterygota, Thysanura, Entotrophi, Collembola, and some Chilopoda are epimorphic, that is, body segments are not added during postembryonic development. In the Pauropoda and Diplopoda several segments and pairs of legs are added during development; usually the first instar has only three pairs of legs! The Protura emerge from the egg with twelve postcephalic segments and pass through four pre-imaginal stages resulting finally in an adult with 15 postcephalic segments (Tuxen, 1949). Symphyla eclose with six or seven pairs of legs and nine postcephalic segments, and after a series of ecdyses the imaginal state is reached with twelve pairs of legs and fourteen postcephalic segments. Some Chilopoda are anamorphic.

7. *Antennae:* The apparent segments have their own intrinsic musculature in the Collembola, myriapods, and Entotrophi. There is no segmental musculature in the flagellum of the Thysanura and Pterygota. The Protura lack antennae.

8. *Gnathocephalon:* In the Pauropoda and probably Diplopoda there are only two gnathal segments—the mandibular and first maxillary; the first maxillae are fused as a complex gnathochilarium. The seven other groups have three gnathal segments. In the Chilopoda the first maxillae are fused as a sort of labium, but in the other six groups the second maxillae are fused as the labium or lower lip of the pre-oral cavity, and the separate first maxillae, like the mandibles, move freely in the cavity. The mandibles have two points of articulation to the cranium in Lepismatoidea and Pterygota; in the Machiloidea, Entotrophi, and the others, there is a single point of articulation.

9. *Tagmosis:* The first three postcephalic segments are grouped into a thorax discrete from the other segments (abdomen), and only these bear the legs in the Collembola, Protura, Entotrophi, Thysanura, and Pterygota (hence—"Hexapoda"). In the four myriapod groups there is no thoracic-abdominal tagmosis. The hexapodous condition is not necessarily a sign of common ancestry; hexapodous Acarina are well known, and the first instar nymph of Diplopoda and Pauropoda is hexapodous and superficially resembles Collembola and larvae of some Pterygota.

10. *Gonopore Site:* In the Chilopoda, Collembola, Protura, Entotrophi, Thysanura, and Pterygota the genital opening is posterior. In the Pauropoda, Diplopoda, and Symphyla it is anterior. However (see above), Tiegs has shown that, at least in the Symphyla and Pauropoda, the progoneate condition must not be given too much weight. It need not imply common progoneate ancestry for these three groups.

11. *Malpighian Tubules:* These are apparently absent in the Collembola and Protura, but present in all of the seven other groups.

12. *Head Folds:* In the Collembola, Protura, and Entotrophi there are lateral outgrowths of the head capsule which fuse with the labium (second maxillae) and enclose all but the tips of the mandibles and first maxillae. None of the other groups are thus "entotrophous." The phylogenetic significance of this condition is obscure, but there seem to be excellent reasons for regarding its origin as independent in each of these three groups.

13. *Cerci:* These are present in primitive Pterygota, Thysanura, Entotrophi, and Symphyla, but absent in Protura, Collembola, Chilopoda, Diplopoda, and Pauropoda. The similarity between cerci of Symphyla and some Entotrophi (Projapygidae) has been regarded as a phylogenetic indicator, but they are enough different so that little emphasis can be placed on them. The similarities of eversible vesicles and certain styli among the Protura, Symphyla, Entotrophi, and Thysanura seem to be of greater importance.

14. *Other Abdominal Appendages:* The midventral collophore of the fourth postcephalic segment is always present in the Collembola and never present in any other group. Its suggested homology with eversible vesicles of Entotrophi and Thysanura is without evidence. The furcula, or spring, usually present on Collembola, has no reasonably clear homology to any appendage known outside the Collembola. If, as has been suggested by Imms and others, the Collembola evolved by paedomorphosis from hexapodous first instar nymphs of a myriapod-like ancestor, then any abdominal appendages like the furcula and retinaculum must be of new origin without leg homologies in other Arthropoda. The only other notable abdominal appendage is the median caudal appendage of the Thysanura. It is probably the fourteenth postcephalic tergite and may be homologous with a similar appendage in Ephemerida.

15. *Germarium:* In the Protura, Entotrophi, Thysanura, Pterygota, and some Pauropoda the germarium is apical; in Collembola, Symphyla, the remaining Pauropoda, and probably the Diplopoda and Chilopoda the germaria are lateral or scattered.

16. *Phallus:* Males of the Thysanura and the unspecialized Pterygota have a distinctive phallic structure with no phallic homologue in any of the seven other groups. The phallus of the Pterygota presumably originated in a protothysanuran, and was first modified for intromission in conjunction with female structures in a protopterygote. Intromittent organs of a radically different kind are found in males of the Pauropoda, Diplopoda, Protura, and Symphyla. The "penis" of Chilopoda is more like that of the Pterygota and Thysanura, but it seems not to be homologous. Recent papers have shown that Collembola and Thysanura do not have intromissive copulation. The details of the exchange of sperm are apparently not known for the Pauropoda, Symphyla, Protura, and Entotrophi.

17. *Ecdysis:* The Pterygota without exception have a physiological mechanism which arrests ecdysis after sexual maturity is reached (the pre-imaginal molt of Ephemerida does not contradict this generalization). In all the eight other groups ecdysis continues after reproduction begins, with the possible exception of the Pauropoda, where Tiegs found no evidence of imaginal molting in the one species he studied.

My view, after several years of self-debate and study of the many discourses in print concerning the relationships of these groups, is that the most justifiable course is not to exclude the Collembola, Protura, and perhaps Entotrophi from the Insecta, but rather to extend the Insecta, almost in the Linnaean sense, to include all nine of these groups in an arrangement approaching the following:

- Subphylum Insecta
  - Section Myocerata
    - Superclass Dignatha
      - Class Pauropoda
      - Class Diplopoda
    - Superclass Trignatha
      - Class Chilopoda

Class Labiata
Order Collembola
Order Protura
Order Symphyla
Order Entotrophi
Section Amyocerata
Class Thysanura
Class Pterygota
Subclass Paleoptera
Subclass Neoptera

The major division separates the Myocerata (with intrinsic antennal musculature, no amnion and serosa, and no phallus or ovipositor of the type uniformly found in Thysanura and generalized Pterygota) from the Amyocerata (lacking intrinsic musculature in the flagellar segments and possessing amnion and serosa and the highly characteristic phallus and ovipositor). This division necessarily splits a vertical series rather than two great groups equally remote from the common ancestor. The Amyocerata are believed by most recent specialists to be descended from a form rather closely related to the Symphyla and Entotrophi. As can be seen, it is not reasonable for entomologists and their textbooks to accept as their province the Collembola and Entotrophi, while rejecting the myriapod groups.

Collembola

Sir John Lubbock, Lord Avebury, beginning ninety years ago, wrote a series of important papers on the Springtails, in one of which he segregated them from the Thysanura and gave the new order the universally accepted name Collembola. In 1873 the Ray Society published his superb *Monograph of the Collembola and Thysanura,* in which all the published knowledge was assembled and analyzed, with many original observations. Lubbock afterward concentrated his interests on other groups of organisms, but he described a few subpolar species of Collembola up to the end of the nineteenth century.

At about this time the taxonomy of the Collembola began to expand, with Tullberg's papers on species of Scandinavia, those of Reuter for northern Eurasia, of Parona for the Mediterranean region, and of Packard for North America. At about the turn of the century the description of new genera and species was rapidly accelerated by several new workers, some of whom are still active: C. Schaeffer, who wrote from 1891–1900 and specialized on the faunas of Germany and subpolar regions; H. Schött, 1891–1931, many regions; G. H. Carpenter, 1895–1935, many regions; J. W. Folsom, 1896–1938, America and the western Pacific; V. Willem, 1897–1925, Europe; J. Carl, 1899–1906, Switzerland; E. Wahlgren, 1899–1920, subpolar regions; C. Börner, 1900–1932, many regions; and W. M. Axelson (later Linnaniemi), 1900–1935, northern Europe. At this time K. Absolon first described many of the remarkable cavernicolous Collembola. Much of the modern classification of the members of the order is the result of Börner's intensive studies. Willem likewise dealt with classification and, particularly, morphology. Other prominent morphologists were R. W. Hoffman and A. Lécaillon. The contributions of J. Uzel, Agnes M. Claypole, and J. Philiptschenko on the embryology are among the most significant. The

Collembola specialists who followed these men have been numerous. Some of the most notable are: R. S. Bagnall, who concentrated on the species of Great Britain and whose Collembola papers appeared from 1909–1941; E. Handschin, 1919–1942, many regions; H. Womersley, 1924–1942, British Empire; and M. Kseneman, 1932–1938, Czechoslovakia. W. E. Collinge, W. M. Davies, and J. Davidson wrote on the physiology and the economic importance of the Collembola of Britain and Australia. There are many taxonomists contributing to the current literature, among the most productive being the following ten. Jan Stach has concentrated since 1919 on the species of eastern Europe and of caves; at an advanced age he is writing a monumental work covering all the known species (the first four parts contain over a thousand pages and 119 plates). J. R. Denis, whose papers have appeared since 1921, has treated the French and Italian forms and has written frequently on morphology of the Collembola; his section on the Collembola, Protura, Entotrophi, and Thysanura is a high spot in the new *Traité de Zoologie* (Tome IX). F. Bonet, now in Mexico City, has been writing on Collembola of Spain, Latin America, and especially of caves, since 1928. J. Agrell's papers on European species, appearing since 1929, have included notable works on the ecology of soil populations. H. B. Mills has written, on the North American Collembola in particular, since 1930; his *Monograph of the Collembola of Iowa* (1934) has long been the basic reference on the North American representatives. E. A. Maynard's *Collembola of New York State* (1951) is, like Mills's *Monograph,* applicable to a wider area than the title implies and includes interesting colored plates and a large bibliography. There are several papers by F. Kos on Yugoslavian springtails. J. T. Salmon has specialized on the Collembola of New Zealand and the nearest islands, with emphasis on their biogeography. H. Gisin, a former student of Handschin, is one of the most notable contemporary specialists of the central European and holarctic Collembola. C. Delamare-Deboutteville publishes regularly papers on the French species and, most recently, on the African. Some other active younger workers are D. L. Wray, K. C. Christiansen, Marie Hammer, and P. F. Bellinger.

The Collembola are so small and so abundant that many are superbly preserved in amber. Handschin (1926) reported in the Baltic Amber only forms similar to those now living. However, the much older Canadian Amber (Cretaceous?) contains a genus which Folsom named *Protentomobrya* and which seems to be annectent between extant groups. The most interesting fossil form is *Rhyniella praecursor* Hirst and Maulik, from the Devonian Rhynie Chert. The recent restudy by Scourfield (1940) seems to show conclusively that *Rhyniella* is a true collembolan.

In spite of the bulk of literature, knowledge of this group is very incomplete. Taxonomically, the Collembola are still relatively little known. Even in Europe and North America the polytypic species concept is only beginning to be applied. The faunas of South America, of most of Asia and the Indies, of western North America, and of much of Africa have hardly been sampled. Almost nothing is understood of the natural history and physiology. Even the process of fecundation of a single species of Collembola was not certainly known until 1952. The embryonic development of a variety of forms needs to be studied by modern zoologists. F. Carpentier and his co-workers have produced important new papers on certain aspects of the morphology of Collembola, but otherwise all too little is yet understood. The cytology and genetics are virtually unknown. Some of the best new research on biology of the Collembola is in the substantial series of papers on dynamics of soil populations and comparisons of populations in a variety of environments. We may expect this area of knowledge to develop rapidly.

Protura

Following Silvestri's discovery of the Protura in 1907 and the publication of Berlese's fine monograph in 1909, perhaps sixty new species have been described. Many are from North America (about 20) and Europe, but Protura have been reported from most parts of the world. There are seven or eight genera variously placed in two or three families. The taxonomic investigations have been the work chiefly of Womersley, Ewing, Condé, Strenzke, Bagnall, and Gisin. Tuxen (1949) has traced the postembryonic development with great care. Otherwise, regrettably little new information on the morphology, physiology, and development of the Protura has been published since Berlese's early monograph.

The most urgently needed investigation is an analysis of the embryonic development comparable to those of Tiegs on *Pauropus* and *Hanseniella.*

Entotrophi

The Entotrophi (also variously called Diplura, Dicellura, Rhabdura, Entognatha, Aptera, etc.) being far more numerous and conspicuous to contemporary collectors than insects in groups such as the Strepsiptera, it is surprising in retrospect to find how tardily they became known. One of Linnaeus' original *Podura* species is supposed by some entomologists to be a *Campodea.* However, the first species recognizably in the Entotrophi is Westwood's *Campodea staphylinus* (1842). Not until 1864 did Haliday describe *Iapyx solifugus,* the first genus and species of the Iapygidae. Some members of this family are about five centimeters long, few are tiny, and they seem to occupy all regions with a mild climate. Yet they went unnoticed until as late as 1864, when an Englishman described specimens he took in southern Italy. The next year Meinert named a second species of *Campodea,* and soon the number of named species of Campodeidae and Iapygidae began to increase materially. Packard described a cavernicolous species of "*Campodea*" from Mammoth Cave in 1871, and at about this time cavernicolous species were being described from Europe.

The third major group of Entotrophi, the family Projapygidae, was discovered in Africa by Cook and named in 1899. Silvestri presented a series of detailed studies of the anatomy of the family during the next few years.

Filippo Silvestri is the one man whose work stands far beyond that of any other specialist on the Entotrophi. From 1898 to 1948 he wrote about ninety papers on Campodeidae, Iapygidae, and Projapygidae. Nearly all are devoted solely to descriptions of new genera and species, and unfortunately Silvestri was particularly remiss in not synthesizing his work from time to time. Only once, in 1905, did he set forth his views on the full higher classification of the Entotrophi and Thysanura. He almost never used keys to species after 1910. Nevertheless, his descriptions and figures are usually recognizable. The number of genera and species named by him is astonishing, in total much exceeding the Entotrophi named by all other taxonomists combined.

The other Entotrophi students of special note have been P. Wygodzinsky, H. Womersley, G. H. Carpenter, J. R. Denis, O. F. Cook, J. W. Folsom, B. Condé, K. Verhoeff, C. Delamare-Deboutteville, and H. E. Ewing, all taxonomists. Womersley (1939) has subdivided the Iapygidae into subfamilies.

The faunas of every region of the world are known in part, perhaps least in the East Indies, Asia, and Africa. The embryology has been presented by H. Uzel, J. Philiptschenko, and O. W. Tiegs. Other morphologists of importance are R. von Stummer-Traunfels, V. Willem, K. Verhoeff, R. E. Snodgrass, and especially B. Grassi. Only fragments are known of the physiology and natural history, other than some noteworthy papers by W. Marten and O. Kosaroff and occasional notes in primarily taxonomic papers. The only recent summary of knowledge is that of Denis in the *Traité de Zoologie.*

The systematics of this order (or subclass) is in a chaotic state. Almost everything concerning its biology remains to be discovered. The anatomy, particularly of the organ systems, is in urgent need of modern investigation. The three so-called families seem to be so different in fundamental structure that their wide separation may become necessary when much more is known of their anatomy and embryonic development.

Thysanura

This class (or order) includes two very different suborders (or orders) which have long been treated as two similar families, the Machilidae and Lepismatidae (Remington, 1954). The former include saltatorial, heavily scaled, free-living, mainly terrestrial forms with large compound eyes. The latter include nonsaltatorial, scaled or scaleless, myrmecophilous, termitophilous, domestic, or free-living forms, some of which are subterranean and lack eyes or ocelli.

The Thysanura have been known well since long before Linnaeus. As with the Entotrophi, the premier worker has been Professor Silvestri. However, for the Lepismatidae and allies the most important publication is *Das System der Lepismatiden,* by K. Escherich (1905). In spite of its age, this fine monograph remains the basic reference, and most taxonomic research since then has been largely an elaboration. For the Machilidae and allies no such revision exists, and each new specialist must try to organize the great number of Silvestri's papers and correlate them with other publications by G. H. Carpenter, Jan Stach, K. Verhoeff, H. Womersley, and especially the very important work of P. Wygodzinsky. Species are known from most parts of the world. Verhoeff (1910) attempted to classify the machiloid Thysanura on the basis of a few genera, with mixed results. General studies of autecology of certain Thysanura by A. Argilas, V. Willem, Eder Lindsay, M. J. Delany, and H. L. Sweetman make this group biologically better known than the Entotrophi and Protura. The recent research on the skeletal morphology and myology by J. Barlet is noteworthy.

The interrelations of Thysanura with other animals are unusually interesting. Carpentier (1940) discovered that the very primitive Strepsiptera, the Mengeidae, parasitize Lepismatidae. Silvestri subsequently described this situation in great detail. While most Thysanura harbor gregarine Protozoa, few other animal parasites have been recorded, none of them insects except for the Strepsiptera. Although there are many genera of myrmecophilous and termitophilous lepismatoids, none has been satisfactorily studied in the field. Among the several domestic Lepismatidae, it is noteworthy that the commonest species, such as *Thermobia domestica* and *Lepisma saccharina,* are unknown in the original wild state.

Although investigated more fully than the Entotrophi, the Thysanura are very scantily known. The physiology and cytogenetics are virtually untouched: tantalizing cases of pattern polymorphism in the machiloids await study; the functions of the eversible vesicles, coxal and abdominal styli, and lateral ocelli are unknown or subjects of controversy. A major revision of the classification is urgently needed. The first of the writer's researches on this problem is in press. In almost any region new species may be found. Natural foods are not well known. Behavioral studies are rudimentary, and only recently have the bizarre methods of insemination of one lepismatid and one machilid been described, respectively by Sweetman (1938) and Sturm (1952).

LITERATURE CITED

Berlese, A.

1908. Osservazioni intorno agli Acerentomidi. Redia, 5:110–122.

1909. Monografia dei Myrientomata. Redia, 6:1–182, 14 figs., 17 pls.

Börner, C.

1901. Vorläufige Mitteilung über einige neue Aphorurinen und zur Systematik der Collembola. Zool. Anz., 24:1–15.

Burmeister, H.

1838. Handbuch der Entomologie. T. II, Abt. II, H. 1, 360 pp. Berlin.

Carpentier, F.

1940. Sur le parasitisme de la deuxième forme larvaire d'*Eoxenos laboulbenei* Peyer. Bull. et Ann. Soc. Ent. Belg., 79:451–468, 12 figs.

Gegenbaur, C.

1878. Grundriss der vergleichenden Anatomie. 2nd ed., 655 pp., 365 figs. Leipzig.

Grassi, B.

1888. Anatomia comparata dei Tisanuri e considerazioni generali sull'organizzazione degli Insetti. R. Accad. Lincei, Mem. Sci. Fis., Mat., Nat., ser. 4, 4:543–606, pls. I-V.

Handlirsch, A.

1903. Zur Phylogenie der Hexapoden. Akad. Wiss. Wien, Sitzber., math.-nat. Kl., 112, Abt. I:716–738, 1 pl.

Handschin, E.

1926. Revision der Collembolen des baltischen Bernsteins. Ent. Mitteil., 15:161–185, 211–223, 330–342, 25 figs., 2 pls.

Imms, A. D.

1936. The ancestry of insects. Trans. Soc. Brit. Ent., 3:1–32, 11 figs.

1939. On the antennal musculature in insects and other arthropods. Quart. Journ. Micr. Sci., 81:273–320, 25 figs.

1947. The phylogeny of insects. Tidj. Ent., 88:63–66.

Latreille, P. A.

1825. Familles naturelles du règne animal. 570 pp. Paris.

LUBBOCK, J.

1870. Notes on the Thysanura. Part IV. Trans. Linn. Soc. Lond., 27:277–297, pls. 45, 46.

MEINERT, F.

1865. Campodeae: en familie af Thysanurernes orden. Nat. Tidskr., 3rd ser., 3:400–440, pl. 14.

PACKARD, A. S.

1883. On the classification of the Linnaean orders of Orthoptera and Neuroptera. Amer. Nat., 17:820–829.

1898. A textbook of entomology. 729 pp., 654 figs. New York.

REMINGTON, C. L.

1954. The suprageneric classification of the order Thysanura (Insecta). Ann. Ent. Soc. Amer., 47:in press.

SCOURFIELD, D. J.

1940. The oldest known fossil insect (*Rhyniella praecursor* Hirst & Maulik)—further details from additional specimens. Proc. Linn. Soc. Lond., 152nd sess. Pp. 113–130, 11 figs.

SILVESTRI, F.

1907. Descrizione di un novo genere d'insetti apterigoti rappresentante di un novo ordine. Boll. Lab. Zool. Gen. Agr. Portici, 1:296–311. 18 figs.

STURM, H.

1952. Die Paarung bei *Machilis* (Felsenspringer). Naturwiss., 39:308, 3 figs.

SWEETMAN, H. L.

1938. Physical ecology of the Firebrat, *Thermobia domestica* (Packard). Ecol. Monog., 8:285–311.

TIEGS, O. W.

1940. The embryology and affinities of the Symphyla, based on a study of *Hanseniella agilis*. Quart. Journ. Micr. Sci., 82:1–225, 9 pls., 41 figs.

1942a. The "dorsal organ" of collembolan embryos. Quart. Journ. Micr. Sci., 83:153–169, 1 pl., 4 figs.

1942b. The "dorsal organ" of the embryo of *Campodea*. Quart. Journ. Micr. Sci., 84: 35–47, 1 pl., 3 figs.

1945. The post-embryonic development of *Hanseniella agilis* (Symphyla). Quart. Journ. Micr. Sci., 85:191–328, pls. 7–12, 29 figs.

1947. The development and affinities of the Pauropoda, based on a study of *Pauropus silvaticus*. Quart. Journ. Micr. Sci., 88:165–268, 275–336, 11 pls., 29 figs.

TILLYARD, R. J.

1931. The evolution of the class Insecta. Pap. and Proc. Roy. Soc. Tasmania (1930). Pp. 1–89, 19 figs.

TUXEN, S. L.

1949. Ueber den Lebenzyklus und die postembryonale Entwicklung zweier dänischer Proturengattungen. K. Danske Vidensk. Selsk., Biol. Skr., vol. 6, no. 3. 50 pp., 74 figs.

VERHOEFF, K.

1910. Über Felsenspringer, Machiloidea, 4 Aufsatz: Systematik und Orthomorphose. Zool. Anz., 36:425–438.

WESTWOOD, J. O.

1838. The entomologist's text book. 432 pp., 5 pls. London.

WOMERSLEY, H.

1939. Primitive insects of South Australia. 322 pp., 84 figs. Adelaide.

ODONATA

Leonora K. Gloyd
Illinois Natural History Survey, Urbana

From a simple beginning as one genus with 18 species (Linnaeus, 1758), the Odonata in 1853 had risen to the rank of a suborder of the Orthoptera and included about 400 species distributed in six major groups. The increase in described species was due largely to the work of Müller (1764), Drury (1773), Fabricius (1775–1798), Leach (1815), van der Linden (1825), Newman (1833), Say (1835–1839), Burmeister (1839), Charpentier (1840), Rambur (1842), Hagen (1840–), and Selys (1831–).[1] Several attempts had been made at classification based on the form of the mandibles, the form of the antennae, and on the possession of aquatic larvae. A start had also been made, by Jan van der Hoeven (1828), on the study of venation and its possible use in classification, and on the study of the genitalia by Rathke (1832). Parts of the European odonate fauna were fairly well known, a few species had been described from most parts of the world, and about twelve papers dealing with fossil species had been published.

It was in 1853 that Baron Edmond de Selys-Longchamps (b. 1813, d. 1900), respectfully and deservedly referred to as the "Father of Odonatology," completed his first synopsis of a subfamily based on the world fauna. The *Synopsis des Calopterygines* was followed by a series of other synopses, monographs, and "additions" (1854–1886) dealing with every subfamily except the Libellulinae. Several of these were in collaboration with his esteemed friend, Dr. Herman A. Hagen. Not only did Selys do a tremendous amount of groundwork in describing species (about 1,119), but he built up a classification using venational, genital, and external morphological characters much as is being done today for other groups of insects. Some of his names, like Legion, Cohort, and Division for higher categories, have given way to universally used terms but his groupings have been supported by ever increasing evidence. In addition to these general works both Selys and Hagen produced many other valuable papers. Toward the close of the century Kirby wrote a revision of the Libellulinae (1889) and a catalogue of the Odonata, including fossil species (1890). In the latter work his principles of nomenclature, the result of much experience and careful consideration, were employed to put the taxonomic work, up to that date, in good order. Type species were indicated, synonyms listed, and a bibliography given for each genus and species. The resultant number of valid species names was about 1,800. Some of the other prominent workers during the Selysian era were Brauer, Cabot, Heymons, Karsch, Lucas, McLachlan, Morse, Packard, Scudder, Uhler, and Walsh.

The first extensive paper on American Odonata was that of Hagen (1861), *Synopsis of the Neuroptera of North America with a List of the South American Species,* which was written at the invitation of the Smithsonian Institution.

---

1. A more detailed account may be found in the papers of Selys (1896) and of Kirby (1901) in which the systematic literature from the time of Linnaeus to the close of the nineteenth century is reviewed.

Since then the most outstanding workers have been Calvert, Williamson, Needham, and Kennedy for the United States and Mexico, and E. M. Walker for Canada. Muttkowski gave us a *Catalogue of the Odonata of North America* in 1910 and Whitehouse one for Canada, Newfoundland, and Alaska in 1948. The Anisoptera part of the *Handbook* mentioned below has been rewritten by Needham and Westfall and is now ready for publication. Special mention should be made of Dr. Walker's two extremely fine, classical monographs of the North American dragonflies of the genus *Aeshna* (1912) and of the genus *Somatochlora* (1925), and of Dr. Kennedy's two much-quoted papers concerning the Odonata of Washington, Oregon, California, and Nevada. Some of the longer papers dealing with state faunas are those of Kellicott for Ohio (1899), Williamson for Indiana (1900), Garman for Connecticut (1927), and Byers for Florida (1930). Mrs. Klots (1932) has treated the odonate fauna of the West Indies, Garcia-Diaz (1938) for Puerto Rico, and Whitehouse (1943) for Jamaica. As yet there is no manual for South American Odonata and to write one soon would be premature because of studies in progress and a vast amount of unworked material. A check list, however, would be quite helpful. Since 1853, Selys, Hagen, Ris, Calvert, Williamson (also responsible for large collections), Kennedy, R. Martin, Förster, Navás, Sjöstedt, Geijskes, Borror, Montgomery, Santos, McLachlan, E. Schmidt, Byers, Longfield, Fraser, Cowley, Gloyd, and others have contributed to a knowledge of the fauna.

The primary work of describing species has continued at a rapid rate throughout the first half of the present century, the number now being in the neighborhood of 5,000, but along with it there have been many studies concerned with geographical distribution, bionomics, nymphs, parasites, morphology and ontogeny of various structures, fossils, monographic revisions, and phylogeny.[2] Some of the greatest advances for the order as a whole may be credited to the following contributions: *Catalogue of the Odonata (Dragonflies) of the Vicinity of Philadelphia, with an Introduction to the Study of This Group of Insects,* by Calvert (1893); *Untersuchungen über die Gestalt des Kaumagens bei den Libellen und ihren Larven,* by Ris (1896), with its phylogenetic conclusions; *Wings of Insects,* by Comstock and Needham (1898, 1899); *Genealogic Study of Dragon-fly Wing Venation,* by Needham (1903); *Collections zoologiques du Baron Edm. de Selys-Longchamps,* the "Cordulines" and "Aeschnines," by R. Martin (1906 and 1908–1910 respectively), and the "Libellulines," by Ris (1909–1919), the latter being a very large and great monograph; *Die Fossilen Insecten,* by Handlirsch (1908), in which a new classification was proposed based on many factors; *The Biology of Dragonflies,* by Tillyard (1917), a superb book written primarily for biologists; *A Venational Study of the Suborder Zygoptera (Odonata) with Keys for the Identification of Genera,* by Munz (1919); numerous papers concerning phylogeny by Calvert, Ris, Williamson, Tillyard, Kennedy, Fraser, Needham, and many others; and the comparatively recent paper published in three parts, *A Reclassification of the Order Odonata,* by Tillyard and Fraser (1938–1940).

Of the many faunal papers some of the most extensive and recent ones for

---

2. See Calvert, *Progress in our Knowledge of the Odonata from 1895 to 1912.* Trans. Second Ent. Congress 1912.

large geographical areas are: *A Handbook of the Dragonflies of North America,* by Needham and Heywood (1929); "Odonata" in *Biologia Centrali-Americana* and *Odonata of the Neotropical Region,* by Calvert (1901–1908 and 1909 respectively); *Libellen (Odonaten) aus der Region der americanischen Kordilleren von Costarica bis Catamarca,* by Ris (1918); "Odonata" in *Die Tierwelt Mitteleuropas,* by E. Schmidt (1929); *The Odonata or Dragonflies of South Africa,* by Ris (1921), "Odonata" in *Catalogue raisonnés de la faune entomologique ou Congo belge,* by Schouteden (1934), and *The Dragonflies of Southern Africa,* by Pinhey (1951); three volumes on Odonata by Fraser (1933–1936) in *Fauna of British India; Manual of the Odonata of China,* by Needham (1930); and *The Dragonflies of New Guinea and Neighbouring Islands,* by Lieftinck (1932–1949). Bartenef has written many papers on the Russian fauna and Valle on that of Finland. Another important work, summarizing almost fifty years of study and rightfully belonging to the century under consideration, is *The Odonata of Canada and Alaska,* by E. M. Walker, of which volume one on the Zygoptera is now in press. Some recent papers on smaller, more or less isolated geographic units are those of Miss Longfield for the British Isles, of Williams and Zimmerman for Hawaii, of Needham and Gyger for the Philippines, and of Asahina, Matsumura, and Oguma for Japan.

For advance in the study of fossil forms from 1853 to 1953 we are indebted to approximately fifty investigators, prominent among whom may be named Selys, Hagen, Heer, Handlirsch, Scudder, Sellards, Cockerell, Tillyard, Fraser, Kennedy, and F. M. Carpenter for their descriptive work and their phylogenetic interpretations.

The greatest collection of Odonata in number of species is undoubtedly that of the British Museum of Natural History and the largest in number of determined specimens is probably that of the Museum of Zoology at the University of Michigan, which houses the collections of Förster, Williamson, and Kennedy. There are many other large and valuable collections in museums and universities throughout the world, some of the best known being the Musée Royal d'Histoire Naturelle de Belgique, the Museum of Comparative Zoology, the Academy of Natural Sciences of Philadelphia, Senckenberg Museum, Deutsches Entomological Institut at Berlin-Dahlem, Austrian National Museum, Zoologische Institut at Halle, Paris Museum, U. S. National Museum, Royal Ontario Museum of Zoology and Palaeontology, California Academy of Sciences, American Museum of Natural History, Indian Museum at Calcutta, Museum Zoologicum of Bogor and Buitenzorg Museum in Java, Australian Museum, South Australian Museum, and the Rijksmuseum van Natuurlijhe Historie in Leiden.

The tremendous growth in knowledge of the Odonata during the past century is due not only to the early foundation on a world-wide basis by Selys and to the work of zealous collectors, but to the strong friendships and cooperation among the leaders who have unselfishly shared their knowledge with all who sought it. Although the systematic study of Odonata stands at a high level of excellence, there is need for time-saving aids in finding out what has been done. A *Bibliographia Odonatologica* was written by Dr. Erich Schmidt but, unfortunately, only one part of this excellent work was printed (1933). As for a catalogue, Dr. F. Ris had a manuscript which he hoped to finish in 1932, but death claimed him in January, 1931. In 1935, J. Cowley, F. F. Laidlaw, and

D. E. Kimmins outlined a program for a complete new catalogue and sought the collaboration of eighteen specialists and the loan of Ris's manuscript. A number of preliminary papers on nomenclature by Mr. Cowley were published but apparently World War II stopped further activity and the work has not, to my knowledge, been resumed.

EPHEMEROPTERA

George F. Edmunds, Jr.
University of Utah, Salt Lake City

Of the estimated 2,000 or more species now known in the order Ephemeroptera, only a few more than a hundred—disposed among 11 genera of the family Ephemeridae—had been named in 1853. No one person, unless it be Pictet, had concentrated any great effort on the group. This is attested by the fact that about twenty-five writers had described species of mayflies, but of these, only Linnaeus, Say, Burmeister, Pictet, and Walker had described more than five species. The trend for nearly two decades remained one of merely describing new species, these new descriptions being primarily furnished by the neuropterists of the period. Genera were poorly delimited and unnatural, and only the European fauna had been investigated in any detail.

The Reverend Alfred E. Eaton must certainly be considered the father of the modern classification of the Ephemeroptera. After writing a number of small papers, he published in 1871 *A Monograph on the Ephemeridae,* which was succeeded a few years later by his monumental *A Revisional Monograph of the Recent Ephemeridae or Mayflies.* It was in this later publication that Eaton's genius for classification was brought to fruition. His division of the Ephemeridae into groups, series, and sections formed the basis of the modern classification. Eaton's concept of the genus was remarkably modern and he consistently designated genotypes throughout the order.

At the turn of the century, just before Eaton's attention was directed away from the mayflies, Dr. J. G. Needham, of Cornell University, started studying the American mayflies. In a series of papers that culminated in 1935 in the publication (with Traver, Hsu, *et al.*) of the book, *The Biology of Mayflies,* Dr. Needham and his students contributed immensely to all phases of mayfly study. At about the same time the eminent mayfly specialist, Dr. Georg Ulmer of Hamburg, Germany, started his study of the Ephemeroptera and subsequently published numerous papers on the world fauna. The publication of his *Übersicht über die Gattungen der Ephemeropteren, nebst Bemerkungen über einzelne Arten* was one of the true milestones in the literature of this order.

The French entomologist, J. A. Lestage, contributed about one hundred papers on mayflies. He had a keen interest in mayfly phylogeny and his endeavor knew no geographic boundaries. He is best known for his extensive work on the nymphs of Palearctic mayflies.

Drs. J. R. Traver, J. McDunnough, and H. T. Spieth have contributed extensively to the knowledge of American species. Dr. Traver is best known as the author of the systematic section of *The Biology of Mayflies.* Dr. McDunnough has described more North American species than any other person, and Dr. Spieth is well known for his phylogenetic studies.

The difficulties of collecting and preserving mayflies have resulted in important collections being established only by specialists in the group. A succession of specialists have built a fine collection in the British Museum (Natural History). Lestage's collection can now be found in the Institut Royal des Sciences Naturelles de Belgique, while it appears that Navás scattered his collection among many museums. Although Ulmer has an extensive personal collection, much of his work has been based on material from various European museums, especially the ones in Berlin and Hamburg. The collection established at the Museum of Comparative Zoology at Cambridge is rich in North American types, as are the Canadian National Collection and the Cornell University Collection.

The recognition of distinct groups within an ancient and apparently declining order such as the Ephemeroptera is not particularly difficult, but because the order is small there has been a continued reluctance to give familial rank to these groups. Such groups have consistently been utilized as the "working units" of the classification, even though they have been ranked as sections, tribes, subfamilies, or families. The history of the recognition of the various groups is relatively simple, but the story of the rank accorded such groups is indeed complex and often bewildering.

The division of the order Ephemeroptera into groups usually regarded as families at present started with Eaton's revisional monograph. Of his fourteen sections, twelve have been raised subsequently by various workers to the rank of family. Thus to Eaton's original arrangement can be traced the families Palingeniidae, Ephoridae (=Polymitarcidae), Ephemeridae, Potamanthidae, Leptophlebiidae, Ephemerellidae, Caenidae, Prosopistomatidae, Baetidae, Siphlonuridae, Baetiscidae, and Heptageniidae (=Ecdyonuridae).

In 1913 Bengtsson proposed that the genera *Ametropus* and *Metretopus* be considered as constituting a separate family, Ametropodidae, and in 1914 Georg Ulmer recognized the distinctness of, and named, the family Oligoneuriidae, a group formerly included in the Palingeniidae.

In the standard American work *The Biology of Mayflies,* Needham applied subfamily rank to the recognized families of European authors. The family Ephoridae (=Polymitarcidae) of the Europeans was divided into two subfamilies, Ephorinae and Campsurinae, the Ametropodidae divided into Ametropodinae and Metretopodinae, and a new subfamily Neoephemerinae, was proposed.

Balthasar (1937) removed *Arthroplea* from the Heptageniidae and placed it in a separate family, Arthropleidae. The soundness of such a move, however, remains to be proved. In the year 1938, Tshernova, and Motas and Bacesco independently proposed the family Behningiidae for the inclusion of the unusual genus *Behningia,* first described by Ulmer and later named by Lestage. The same year Lestage considered *Behningia* to be a member of the Oligoneuriidae and reduced Behningiidae to synonymy of Oligoneuriidae. Demoulin has recently reinstated, I believe correctly, this monotypic family. In 1938, Lestage also proposed a new family, Siphloplectonidae, but in the writer's opinion the division is unnatural, and Siphloplectonidae is a synonym of Metretopodidae.

In his fine report on the mayflies of the Sunda Islands, Ulmer proposed a new subfamily of Siphlonuridae, Pseudoligoneuriinae, for *Pseudoligoneuria,* known only from an oligoneurid nymph whose incipient venation appears to be of the siphlonurid type. In 1943, Spieth transferred the subfamily to the Oligoneuriidae. Only three years before his death in 1945, Lestage proposed creation of the family Tricorythidae for a group of genera bearing remarkable convergent similarity to the Caenidae. The most recent proposed change in the classification is the relegation of Metretopodidae to a subfamily of the Siphlonuridae by Demoulin in 1952, but the desirability of such a move seems questionable.

The families have had a stable existence when compared to groupings above family level. As with the families there has been little agreement on the taxonomic level given such complexes of families. They have been ranked as groups, subfamilies, families, superfamilies, or suborders. Oddly enough, the great majority of all workers have regarded the mayflies as being of three great sections, although two, four, five, or six have been indicated by others. But there has been little agreement on the composition of these groups, and, with our present knowledge, stability is neither expected nor desired for some time to come.

As in most orders, the preponderance of the papers on Ephemeroptera has been dedicated to a limited area of the world, and thus, though there are great gaps in our knowledge, some areas have become well known. As is to be expected, the western Palearctic region is best known, as a result of many fine papers produced there by the numerous authorities. The eastern Palearctic region has been rather neglected by comparison. Except for studies of some of the Indian mayflies and the fine works by Ulmer on the Sunda Islands, the Oriental region also has been rather neglected. The Australian and New Zealand species have been reported upon by several competent specialists, but revisions are needed of this critical fauna. The mayflies of the Ethiopian and Neotropical regions are known chiefly from specimens that have come to the cabinets of European and American workers, but exceptional regional studies have been done on South Africa, Brazil, and Porto Rico.

The North American mayfly fauna is certainly one of the most extensively studied, but great geographical areas remain unworked. The first detailed study upon the mayfly fauna of any state was done by J. R. Traver in North Carolina, and other detailed studies have followed, the most notable being the recent reports on the Florida fauna by Berner and the Illinois form by Burks. Drs. McDunnough and Ide also have made extensive studies in certain parts of Canada.

Aside from the need for collecting and describing the mayfly fauna of the little known geographic areas of the earth and continuing the description of immature forms, there are many other fertile fields of study on this order of insects. Phylogenetic studies are most desirable. The present arrangement of families leaves much to be desired, and the grouping of families into larger groups is not satisfactory. Instead of confining studies by setting geographic boundaries, future workers will find it more productive to confine themselves to a systematic unit and ignore political subdivisions. Revisions of many genera are sorely needed; for example, I am aware of three congeneric species that are now referred to three separate genera and I suspect that one or more species bears the alias of still a fourth genus. Distinct races exist within many species of mayflies and in some genera the problem of naming and making known these races and the causative factors of their formation and present distribution is very pressing. This inevitably leads to the problem of obtaining larger samples of specimens, topotypes of older species, and especially reared series. As representatives of an ancient group of insects that are, because of their short adult life and tendency to desiccation, seldom dispersed any great distance by air, mayflies are prime subjects for biogeographic studies. For those willing to meet the special problems of collecting and preserving the insects of this order, there is a promising field of research.

PLECOPTERA

PER BRINCK
Lunds Universitets Zoologiska Institution

The history of our knowledge of the stoneflies is comparatively short. Not until late in the Middle Ages are they even modestly mentioned in the literature. Some authors of the sixteenth century dealt with them as *grosse Wassermücken* (big water flies). In 1603 in his *Theriotropheum Silesiae* Caspar Schwenckfeld described a perla as *Musca caudata.* Moufet in 1643 *(Insectorum sive Minimorum Animalium Theatrum)*, J. Johnston in 1653 (*Historia Naturalis de Insectis, Libri III*), and J. Wagner in 1680 (*Historia Naturalis Helvetiae Curiosa*) describe a *Musca aquatilis aestiva major* which is also a perla. In the literature of the eighteenth century, stoneflies were mentioned more often, but they had no name of their own until much later.

It is true that *Perla,* a name which has long been applied to a genus of well-known European stoneflies, appeared as early as 1602 in Aldrovandi's *De Animalibus Insectis Libri VII.* But it did not refer to a stonefly, for at that time perla was the common name for dragonflies, the larvae of which were known as *Libella fluviatilis.* Moufet (*op. cit.*) recognized the association between the larvae and the imagines and restricted the name *Libella* to Odonata. For some time *Libella* and *Perla* were used side by side (cf. Goedaert: *Historia Insectorum Generalis,* several editions), but in the eighteenth century we meet with *Libella* only. *Perla* disappeared as a generic name until it was revived by E. L. Geoffroy in 1762 (*Histoire abrégée des insectes*) and by Cuvier (1798), and P. A. Latreille (1802) made it the type of a section or family Perlariae among the Neuroptera.

Stoneflies were figured early. There is an excellent illustration of a perla in G. Hoefnagel's *Archetypa Studiaque* (1592) and *Diversae Insectorum volatilium* (1630). No text accompanies the figures.

The number of pre-Linnaean species of Plecoptera is very small and they cannot be identified with any certainty. Linnaeus and his pupils and the Linnaean epigons produced scattered descriptions of stoneflies, but most of them are poor and rarely allow identification without examination of the types.

The beginning of our knowledge of North American stoneflies was made by Thomas Say, who described four species in 1823 (*Godman's Western Quarterly Reporter,* Vol. 2, no. 11).

In the 1830's Edward Newman of England started detailed work on the Plecoptera. But the first person to make a thorough study of the group was the Swiss F. J. Pictet. In his *Histoire naturelle générale et particulière des insectes Néuroptères,* he devoted 423 pages and 53 plates to the Plecoptera. This was an important work, presenting much information on the morphology, anatomy, biology, and taxonomy of these insects. Pictet also showed that the nymphs are quite different from the larvae of the caddisflies, contrary to the views of previous authors. The first description of the postembryonal development of a perla, by de Murault in 1683 *(Ephemerides Naturae Curiosorum)* had been forgotten.

About 1853 approximately 150 species of stoneflies had been recognized—though not adequately described. There were many more names available but the technique of studying these insects had advanced very little and many of the descriptions could not be interpreted. Pinned specimens often shrink and change color, so the superficial diagnoses of that time, giving color and rough external structures, were not very useful. The general classification of the group was still undeveloped. Most of the described species were central European. Scattered descriptions of species from other parts of the world had appeared but no definite zoogeographical views could be formed.

This state of affairs continued throughout the nineteenth century. Several authors described new species but few of the descriptions were adequate. No clear conception existed with regard to the limits of the species. During this time the first comprehensive review of the American fauna was given by H. A. Hagen in his *Synopsis of the Neuroptera of North America* (1861).

A sound basis of study developed when workers began to use genitalic characters. A. Gerstächer in a paper on Plecopteran gills (1874) had attempted the first description of the genitalia of a *Nemoura* sp. but it was not until the 1890's that taxonomists began in earnest to clarify the subject by means of this method. In 1894 K. J. Morton based a study of European nemouras on male genitalia. Fr. Klapalek in 1896 wrote a fundamental paper on the genitalia of stoneflies. P. Kempny dealt thus with the genus *Leuctra* in 1898, and in 1902 F. Ris published a monograph on the central European nemouras, based on KOH preparations of the male and female abdomina. The investigations proved that in many genera the male genitalia are very diverse and offer excellent specific characters.

A classification of the stoneflies was practically nonexistent until Klapalek in 1905 placed the Hungarian species in two suborders and six families, primarily based on the structure of the palps and the cerci. In 1909 G. Enderlein presented a more elaborate classification, based on all genera adequately described at that time (40). He distinguished two suborders and five families, dropping three of Klapalek's units.

Klapalek wrote seventy papers on stoneflies. Several of these monographs dealt with genera or families and are still of great value. It is a pity, however, that he did not use KOH preparations or a similar method, instead of describing the genitalia of dried specimens. The twentieth century has produced several fine taxonomic works on the stoneflies of various countries. Needham and Claassen in 1925 presented a monograph of the North American species, and this was followed by a volume on the nymphs by Claassen in 1931. In a series of fine publications Th. H. Frison added greatly to these dicussions. Similar studies have been published by Hynes and Kimmins in England, Despax in France, Aubert in Switzerland, Kühtreiber in Tyrol, Brinck in Scandinavia, Kohno, Okamoto, and Ueno in Japan, Wu in China, Tillyard in Australia and New Zealand, and Barnard in South Africa.

Ecological studies began with an investigation of the nymphs and the recording of flight periods and other periodicities of the imagines. E. Schoenemund in the 1910's and 1920's laid the foundation for ecological studies but, little followed until H. B. N. Hynes's and P. Brinck's monographs (1941 and 1949 respectively).

A milestone in plecopterology was the publication in 1940 of the *Catalogue of the Plecoptera of the World,* by P. W. Claassen. It contains a bibliography, which has been brought up to date by a "First Supplement," edited by J. F. Hanson and J. Aubert in 1952.

In the future there is very much to be done among the stoneflies. Primary taxonomy on a critical basis is needed from many parts of the world. Monographs of genera and even higher categories are much to be desired. We know about 1400 species and 138 genera; but of these about 300 species and at least 30 genera are doubtful. This is to a considerable extent due to the work of R. L. Navás who, in many publications, presented numerous descriptions differing little from those produced by most of the authors of the eighteenth century.

Further, the present classification cannot be considered settled. W. E. Ricker's *Stoneflies of Southwestern British Columbia* (1943) and his *Evolutionary Trends in Plecoptera* (1950) are fine works but what is needed is comparative morphological investigations like the excellent study of J. F. Hanson on the Capniidae (1946). The incongruity between the knowledge of the two best known faunas, the North American and the European, is marked as regards certain families and genera.

Anatomy, histology, and physiology are very little worked fields. There is a classic paper in C. F. Wu's volume on the structure and behavior of *Nemoura* (1923) but other works of this type have not followed. Ecology is a virgin field in many respects, and should be particularly profitable in North America, with its highly varied plecopteran fauna which is one of the richest in the world. Zoogeography is a fascinating subject in this group, of which certain genera have changed very little since the Permian period and still occupy almost the same regions. The geographical grouping of genera and species and their relationship will be very important in deciding the origin and development of the freshwater faunas.

Briefly, the stoneflies promise many exciting discoveries to present and future students—but at this time taxonomy remains a formidable obstacle to progress.

EMBIOPTERA

Edward S. Ross
California Academy of Sciences

Until very recently the Embioptera have never received serious specialized study. Most of the past literature concerning this small order of secretive insects has been but an incidental by-product of larger systematic projects of the authors concerned. There are several reasons for this. First, the order barely ranges into Europe or the United States, the regions from which most systematic studies have emanated. Second, no limited area possesses sufficient species to warrant a regional study, and no species are known to be of economic importance. Finally, the accumulation of specimens in museums is scanty and scattered. Few entomologists ever see Embioptera on their field trips, let alone collect them. When they do, they tend to secure only juvenile specimens, which are of no value in the present period of systematic studies.

Latreille in 1825 was the first to mention an embiid in the literature. Not until 1832, however, was a species actually named. This was *Olyntha Braziliensis* Gray. In 1837 Westwood named two more species, one of which was based on a figure published by Latreille in 1829. Burmeister (1839), Rambur (1842), Hagen (1842), Blanchard (1845), Lucas (1849) are the authors who wrote about these insects before 1853. By then eight species names had been proposed, of which two were very early and correctly suspected to be synonyms.

In 1853 orders as we know them today had not yet been fully defined, but it is evident that the distinctiveness of these insects was very early recognized for Burmeister placed them at a group level comparable to the termites. Lucas (1849) was the first to note that the embiids live in silk tunnels. The location of the silk-spinning organs was an unsettled question; as recently as 1912, Enderlein stated that the glands involved were maxillary. Previously Grassi (1889) and Melander (1902) had correctly located these organs in the fore tarsi.

Hagen (1885), Krauss (1911), Enderlein (1912) each compiled the existing knowledge of the order in monographs. Navás (1918) reviewed the South American species in a single treatment. None of these workers had much, if any, field knowledge of the Embioptera. It may be concluded that almost all this work suffered from a failure to make good microscope preparations of the male abdominal terminalia and to utilize properly the complicated details of these structures in classification. Too much emphasis was placed on easily accessible wing venational characters, particularly the branching of the radial sector. It is now evident that one type of wing venation has independently developed on at least three different evolutionary lines. Apterism in the male also led to confusion in defining genera. Navás added to the burden of future students by occasionally basing new species on females or juvenile forms.

Consett Davis in 1936 commenced an intensive study of the Australian Embioptera and described the genus *Metoligotoma* comprising a surprisingly large array of species and subspecies based on good characters in the male genitalia. Earlier workers, however, would certainly have regarded these, on the basis of superficial features, as only one species. Until his accidental death in 1944, Davis continued and expanded his interest to a world-wide scope. His *Taxonomic Notes on the Order Embioptera* which appeared in twenty parts (1939–1940) was based on a study of the types of many species. Unfortunately the pressure of approaching military service caused him to do this work more hastily than desirable.

At the present time less than 300 species of Embioptera are known. There is evidence, however, that the order may eventually prove to comprise about 1,000 species. The writer feels this challenge is worth a lifetime of concentrated study. He is now making field trips to various parts of the world with the principal purpose of collecting and observing these insects. The discovery and description of hundreds of new species necessary before the basic classification can be fully developed, will take a long time. Semiarid regions, such as parts of Mexico and Africa which are biotically related to adjacent humid tropical regions, are proving particularly rich in species. Burma, an eastern frontier in the dispersal of the large family Embiidae (centered in Africa), should be visited by an embiopterist.

All future studies must include a very detailed exposition of male abdominal terminalia characters. The writer's current studies in African and New World species indicate, however, that these characters may at times serve only to define species or racial groups whose members are separable on more superficial features, such as size, color, and minor details in form.

As the Embioptera become well sampled, the difficulty of defining species is certain to increase. Generic concepts, so dependent on the consistency of the array of component species, may be expected to change frequently, for Embioptera studies are yet in an early formative stage.

ZORAPTERA

Ashley B. Gurney
Entomological Society of America, 1530 P Street, N. W., Washington 5, D. C.

The Zoraptera comprise one of the most recently defined insect orders. As recently as 1913 Silvestri described the first three species and characterized the order. Several years earlier, American entomologists had collected Zoraptera and were puzzled concerning their identity, but it was not until 1918 that the first nearctic species, *Zorotypus hubbardi* Caudell, was described. Prior to Gurney's 1938 synopsis, Silvestri, Caudell, and Karny had described 12 species. Following World War II, two French entomologists, Delamare-Deboutteville and Paulian, have described several species from Madagascar, Mauritius, and Africa. At present there are 22 described species, in addition to several undescribed ones in collections. One family, Zorotypidae, and one genus, *Zorotypus,* are known. An Indian genus, *Menonia* George, proposed as zorapterous in 1936, appears to be incorrectly placed.

Very few collections contain more than an occasional species. In types, number of species, and total number of specimens, the United States National Museum has much the best representation, though the Silvestri material at Portici is significant, and that recently studied by Delamare is important. Valuable recent material also belongs to the Bernice P. Bishop Museum, Chicago Natural History Museum, and the California Academy of Sciences, owing mainly to the field work of E. C. Zimmerman, Henry S. Dybas, and E. S. Ross, respectively.

Silvestri's work included detailed descriptions and sketches of setal patterns, but it is sometimes difficult to recognize critical specific differences from his papers. Caudell was the first to describe winged individuals. His descriptions are brief and clear. Gurney developed the significance of concealed male genitalia, stressed the preservation of most material in alcohol, and brought out the first comprehensive review (Proc. Ent. Soc. Washington, 40:57–87, 1938).

Zoraptera are widely distributed in the tropical and warm temperate areas of both hemispheres, including many small islands far from continents, but are not recorded from the mainlands of Australia, Asia, and Europe. They were first thought to be inquilinous with termites, but that frequent association is now known to be correlated with preferences for similar environments rather than a close social relationship. Crampton was much impressed by the apparent phylogenetic relationship to psocids (Corrodentia), and Delamare's recent contributions on external sclerites and weakly defined castes indicate close relationship to termites. Information on biology has gradually grown, owing mainly to the observations of T. E. Snyder, H. S. Barber, and other associates of Caudell, to Gurney's notes, and to recent studies by Delamare. Zoraptera are not known to be of any economic importance.

We may expect the steady growth of knowledge about species and their distribution. Possibly other genera will be found. Diligence and knowledge of how to look for and recognize Zoraptera are rather essential to effective collecting. Detailed biological work is needed, and a comprehensive study of the morphology in comparison to that of termites and widely separated families of psocids may be quite revealing as regards phylogeny. A student on such a problem should be advised by someone acquainted with psocid classification, so that obscure psocid groups may be consulted.

SOME MINUTE INSECTS: ANOPLURA, MALLOPHAGA AND THE SCALE INSECTS

G. F. Ferris
Stanford University

Gorgeously colored butterflies and glittering beetles were for long the primary objects of interest to entomologists, with the flies and bees and wasps in a somewhat secondary place. All of these insects fulfilled the common desire of collectors to possess objects of beauty and curiosity which could be displayed to admiring onlookers. This circumstance, in addition to the fact that minute forms could not be examined with the hand lens, led inevitably to the result that the interests of entomologists were long centered upon these larger and aesthetically more pleasing insects. The minute, dull-colored, and, to the unaided eye, unimpressive forms—actually perhaps the majority of insects—have always been much neglected and it is only in comparatively recent times that most of them have begun to attract any special attention. Even today only a relatively small number of entomologists concern themselves especially with such forms.

As long as entomology remained primarily an expression of aesthetic feeling this neglect was general. Then, with the growing appreciation of the economic and biological interest of many of these small forms, their study began to expand. The economic importance of the scale insects (Coccoidea) and other small pests of agriculture and the recognition of the importance of the sucking lice in the transmission of disease led to the study of these groups and this interest has spread to other small forms. Even so, the microscopic insects—to which may arbitrarily be assigned insects less than five millimeters long—have never received the attention they deserve.

Apart from purely aesthetic considerations, the difficulty of studying these minute forms has been a determining factor in causing this neglect. They cannot be studied satisfactorily from pinned specimens, even from specimens mounted on minute pins or points and even with the aid of the improved microscopes which we possess today. They require special methods in making preparations that can be examined by transmitted light under the powers of the compound microscope. Only as these methods have developed could any real understanding of such forms be gained.

Throughout his entomological career the writer of these lines has been interested almost exclusively in these microscopic insects. He must confess to being irritated by any insect on a pin; why not mount it on a microscope slide, where it is possible to see what is actually on the insect, if the preparation be properly made? His interests have been largely confined to insects which must be so mounted if they are to be studied at all with any degree of satisfaction. More than thirty-five years of experience with the scale insects and the two groups of lice, with an occasional excursion into other groups of small forms, has served only to increase his impatience with insects which cannot be so studied. If the whole insect is too large to go on a microscope slide, it can be divided so that its parts can be so mounted. Even students of the Lepidoptera, in spite of their reluctance to "ruin a specimen," have learned to place the genitalia of the males upon microscope slides. But still the great majority of all insects, almost regardless of their size, are mounted on pins, even though little can be learned from such specimens. It is quite true that for the larger forms this is probably the quickest way to prepare them and possibly the easiest way to study them, but even such forms must sometimes be torn to pieces and reduced to a condition in which microscopic study is possible. Naturally no one would advocate attempts to put *Morpho* butterflies on microscope slides! But, after all, large forms like these and the rhinoceros beetles are not all the insects. There are whole hosts of minutes flies, minute beetles, minute parasitic Hymenoptera, and many other groups which can best be treated as microscopic insects should be treated.

Along with this matter of properly preparing specimens for study goes the closely related matter of how to communicate to others the results of such study. In other words, making suitable illustrations is equally a part of any work on such forms. Here again, we must to a degree forget about any purely aesthetic considerations. We must think merely of communication, for there is in such specimens little artistic appeal. The present writer has been especially concerned with developing methods of illustration which are peculiarly suitable for this type of work.

This paper, however, is not intended as a manual of methods. Its purpose is to review the century's progress in the studies of the minute insects. But we may legitimately call attention to the fact that this progress has depended entirely upon the development of the methods discussed above. It is a sound generalization to say that, in approaching such groups, the suitable solution of these problems of method is at least more than half the whole process. The dawning recognition of this fact constitutes a large part of the story of progress in the study of the groups to be discussed here.

The Scale Insects (Homoptera: Coccoidea)

Agriculturalists in California, Florida, and some other parts of the world will be fully aware of the importance of these insects, for they are, in these areas, among the most important of insect pests. In fact, horticulturists and greenhouse operators almost anywhere will have had some experience with them. They are almost all very small and this has been a significant factor in the development of our knowledge of the group. The determination of the various species is at times a matter of very great importance, but their positive determination was long impeded by their diminutive size and by the failure to employ proper methods, first in preparing them for study and then in illustrating them in order to communicate the bases for their recognition.

Certain aspects of the study of these groups are frequently confused. There is a confusion between the fact that an insect has been named and the idea that it has been described; again, there is a confusion between the fact that an insect has been briefly described and the idea that it is "known." Approximately three thousand species of scale insects have been named; relatively few of these are in any real sense described and still fewer can be regarded as known. Actually, a small percentage of the named species of scale insects are so described that they can be identified positively from the original description alone. It is only in recent years that methods of preparing these insects for study have been such that they could be satisfactorily illustrated and perhaps even more recently that proper methods of illustration have been developed.

The story of the growth of our knowledge of the systematics of this group is somewhat as follows. Linnaeus, in his *Systema Naturae,* recognized only one genus of this group, the genus *Coccus.* To this genus he referred 22 species. In 1784 the genus *Orthezia* was named, but for many years every one of the few other species of this group that were described was referred to the genus *Coccus.* Then in 1833 the genus *Aspidiotus* was named for all the forms which we now call the family Diaspididae and in 1835 there was named the genus *Diaspis,* from which the family name Diaspididae was derived. A very few genera were named during the first two thirds of the nineteenth century, these almost always for some peculiar form such as the genus of the lac-producing scales, the genus of the cochineal insects, the genus whose only known member produces the white wax much used in China, and the genus of the strange "ground pearls." But it was not until 1868, more than a hundred years from the time of Linnaeus, that Signoret and Targioni-Tozzetti—the one in France, the other in Italy—added greatly to the known forms. In a catalogue published in 1868 Signoret listed a total of just over 300 known species, which he placed in the scale insects, and at the close of his work, in a list of genera, many of them established by him, he records approximately 70 names, of which a few are synonyms. It is from this work that any especially serious attempt to understand the scale insects dates.

It was perhaps this work which stimulated a number of workers on this group during the period from 1869 to 1900. These included Comstock, whose reports on scale insects were the first examples of an approach to clear and understandable illustrations of a small number of species. There was Maskell, working in New Zealand, who, in a series of papers beginning in 1878 and ending in 1898, described a large number of forms, few of which, unfortunately, can be identified from his descriptions and very inadequate illustrations. There was Cockerell, in the United States, who described numerous species and whose work, almost entirely without illustrations, did little more than indicate that scale insects existed on certain hosts in certain areas. There was the work of Newstead, continued long after 1900 and best known through his *Monograph of the Coccidae of Britain,* which appeared in two volumes (dated 1901 and 1903) and attained a standard of usableness closely approaching the standard with which we might be satisfied today. There was the work of Green, which culminated long after 1900 in the five volumes of his *Coccidae of Ceylon,* a work most beautifully but inadequately illustrated. There was the work of Leonardi, begun in the 'nineties and continued until his death in 1918, which never rose much above the minimum of enduring value. And there were various minor students whose work was in no way notable.

Altogether, however, the number of species and genera that were at least brought to notice greatly increased, rendering the publication of a comprehensive catalogue desirable. In 1903 such a catalogue was published, the result of a huge labor of compilation carried through by Maria Fernald. In this she listed 1,514 species that had been named up to that time. This publication marked a most important step in the development of our knowledge of this group and is still an invaluable work of reference.

After 1900 there followed a period in which a considerable number of students of the scale insects appeared and the literature grew rapidly. From 1906 to 1915 supplements to the Fernald catalogue were published, the last of these, by E. R. Sasscer in 1915, bringing the total number of described species to more than 2,100 names. Since that time there has been no accounting, but the number of described species must now total almost or quite 3,000.

It is clear that the scale insects, now rather generally accepted as a superfamily, the Coccoidea, are actually an enormous group. If we may form any valid opinion on the basis of the number of species that have been described from parts of the world where collecting has been done with some care, it may be surmised that the named species number perhaps no more than one tenth and certainly no more than one fourth of those which actually exist. In other words, there are probably from 12,000 to 30,000 species of scale insects in the world.

It is evident that sound and usable basic work on these mostly microscopic forms is imperatively called for. Unfortunately, much of our present knowledge is merely names, for only a relatively small portion of the named species can definitely be recognized on the basis of the existing work. It was not until about 1915 that methods of preparing material were developed which would make it possible to see everything that is to be seen upon these insects and that a realization of the need for a genuinely suitable method of illustration developed. Thus an important part of the work now before students of the group is the elucidation of the mass of unidentifiable species, their proper illustration, and their arrangement in genera which have some relation to the realities and will make possible a fuller understanding of such problems as the geographical distribution of the groups and species.

In the last twenty-five years especially, significant progress has been made. The study of the Coccoidea has passed very largely from untrained amateurs who might be called simply "naturalists" to a smaller but more competent group of students with a definitely professional point of view, who are beginning to achieve some results in the program of basic studies. The genera are being elucidated as rapidly as circumstances permit and we are approaching the time when students of the future will have a sound foundation on which to build.

The Anoplura or Sucking Lice

The Anoplura constitute another group which can be studied only from material that has been properly prepared for examination under the compound microscope. Almost all of the species are less than five millimeters in length. Moreover, most of them are quite delicate forms which shrivel badly if they are preserved in the dry condition.

These, especially, are forms which have no attraction for those whose interests are determined by aesthetic considerations. As far back as 1842 a writer remarked that he had often been rebuked by his friends for entering upon the study of a group of insects whose very name was sufficient to excite feelings of disgust. Hence the group received but little attention until about 1900, and as late as 1908 a catalogue of the order listed only 65 species. We now know between 225 and 250 species, probably about half of those in existence.

The connection of these insects with the transmission of disease makes the group especially important, and the proper description and illustration of the various species, which alone will make possible their precise identification and a knowledge of their distribution and of their hosts, is urgent.

The sucking lice have long been known because of the occurrence of two of their species upon man himself, but as a group they also were long confused with other wingless insects. Thus Linnaeus, who applied the old Latin name *Pediculus* to them as a scientific name, included under this name a large and weird list of species, many of which actually belong to quite different groups. It was not until 1806 that the distinction between the biting lice and the sucking lice was recognized and the biting lice were placed in a separate genus. Not until 1815 were the sucking lice themselves divided into three genera, not until 1844 was a third genus named, and not until 1871 was a fourth genus established. As late as 1904 only seven genera had been named and one of these did not belong to the sucking lice. Even as late as 1908 only 65 species were known. In 1916 a catalogue of the group listed about 120 species and since that time the number of known species has almost, if not quite, doubled.

Until about 1915 the study of this group was handicapped by the lack of any knowledge of the proper preparation of specimens for study, but about that time methods became available which now make the examination of species of this group quite simple.

Correlated with the difficulties of the study of species has been the curious history of the development of a system of classification. As already noted, Linnaeus included the sucking lice, along with many other forms, in the genus *Pediculus,* which was placed in the order Aptera. They were then placed by Fabricius in the order Antliata, along with another miscellaneous group of forms. Then, in 1806, Latreille established the order Parasita for the biting lice and sucking lice. In 1815 the order Anoplura was named for the lice by Leach. In 1874 the sucking lice were placed by Giebel in the Hemiptera, and since that time various ordinal names have been employed for them. The idea that the sucking lice are connected in some way with the Hemiptera long persisted.

Of recent years the principal difference of opinion concerning them is whether they should be united once more with the biting lice into a single order or whether two orders should be maintained for these two groups. The writer holds that they should be separated into two orders, the name Anoplura being employed for the sucking lice.

The writer's interest in this group, continued over many years, culminating with the publication in 1951 of a volume, entitled *The Sucking Lice.* The general classification of the group into families and subfamilies is still unsatisfactory and must remain so until a larger number of species have been found.

The Mallophaga or Biting Lice

The order Mallophaga is another group of mostly quite small forms which can be studied only from microscopic preparations. Fortunately, most of the species are quite darkly pigmented and do not need to be stained, but they do call for proper preparation if their characters are to be appreciated, and they, like other microscopic insects, have suffered from the lack of interest in the development of methods of preparation.

The Mallophaga are primarily bird-infesting forms, only a relatively few species occurring on mammals, and these bird-infesting species have never aroused quite the same feelings of repugnance which have commonly been felt toward the sucking lice. Since birds have been favorite subjects for study, the Mallophaga have attracted a good deal of interest.

The early history of the group, however, is involved with the sucking lice and it was not until 1806 that a distinction between the two groups was noted, although they were placed in the same order. Some time between 1840 and 1845 Burmeister named the order Mallophaga and it has been maintained quite consistently ever since.

Three great events in the group's early history should be recorded. In 1842 appeared Denny's *Monographia Anoplurorum Britanniae,* in which many of the species were described and illustrated. In 1875 came Giebel's *Insecta Epizoa,* a still more important work. In 1880 Piaget's monumental *Les Pediculines* and its supplement were published. There have been no comparable works since that date. Beginning in the 1890's the center of work on this group was transferred to North America, with the various papers, some of them quite extensive, published by Vernon L. Kellogg, the most important of these being published under the auspices of the California Academy of Sciences.

It must be noted that until recently the classification of the Mallophaga has not been especially satisfactory. The earlier workers, including Kellogg, were extremely conservative; also, they knew no more than other students of microscopic insects about the proper preparation of material. Fortunately, specimens of Mallophaga could be studied with somewhat greater facility than some of these other groups even with inadequate preparations. After Kellogg, a number of students of the group in various parts of the world began describing new genera, with apparently little consideration of the work being done by others. Some of these workers had access only to inadequate collections; also, the competence of some of them may be seriously questioned. The result was that the classification of the group fell into a distressing disorder, from which it is only new beginning to emerge.

The recent publication of a comprehensive catalogue of the Mallophaga by Clay and Hopkins, in which the authors have attempted to clear up much of the confusion in the synonymy of the genera, once more places the study of the Mallophaga back on a reasonably smooth road to further development. Also there should be mentioned the recent comprehensive treatment of the Mallophaga of mammals by Dr. Fabio Werneck which will give future workers on these species something sound to build upon.

Résumé

Through the story of the study of these three groups runs a common thread—the need of developing proper methods by which these insects can be studied. That thread will be found to extend also through the story of many other groups of microscopic insects. Not until the recognition of this need becomes widespread and a knowledge of proper methods is more widely distributed will the study of such groups attain its ultimate possibilities of achievement.

PSOCOPTERA (CORRODENTIA, COPEOGNATHA)

K. M. Sommerman and J. V. Pearman
Orlando, Florida, and Aston Clinton, England, respectively

In 1853 knowledge of psocids was meager, being contained in about thirty publications by European authors. Descriptions were inadequate and dealt with trivial superficialities. If allowance is made for synonymy, less than 50 species (in 7 genera) were known, including possibly 8 from the Western Hemisphere.

Psocids were first segregated as a unit group (*Psocus*) in Neuroptera by Latreille (1794, France). Then Leach (1815, Scotland) set up separate divisions for winged and wingless forms. Although wing venation had been used for grouping by Stephens (1836, England) and Burmeister (1839, Germany) it had been utilized only twice—by Curtis (1837, England) and Burmeister—in generic diagnoses.

The period from 1853 to 1903 was marked by the establishment of wing venation as the prime factor in generic differentiation. This was accomplished mainly through the influence of the pioneer studies of Hagen (1849–1886; Germany until 1870, thereafter U. S.). His bibliographical research, his monographs on wingless psocids and fossils in amber, as well as much descriptive work and a full synonymic synopsis with terse generic diagnoses, paved the way for later advances. In this country new species were described by Walsh (1862), Aaron (1883–1886), Packard (1889), and Banks (1892–1901), but the contributions of a wider scope were still being made by European workers, notably by McLachlan (1866–1903, England) and Kolbe (1880–1888, Germany). The latter, a Darwinian disciple, having fancied resemblances with stages of evolutionary development, proposed a classification in five sections, which failed, however, to supersede Leach's simpler arrangement. Comstock (1895, U. S.) questionably limited the order Corrodentia to psocids. So at the close of this fifty-year period the psocids held family or superfamily rank in the order Neuroptera. About one hundred fifty papers had appeared, most of them concerned with systematics, a few with biology and general morphology.

Two overlapping phases of nearly equal extent can be recognized in the period from 1903 to 1953, during which the number of described species increased rapidly. In the earlier phase the quality of the systematic papers continued at about the same level as previously, but there was an increase in their quantity and in their geographic range. The firm establishment in 1903 of a suborder (Copeognatha) for psocids exclusively marked the beginning of a prolific period for Enderlein (1900–1936, Germany). Much of his work is especially valuable because it consists of regional or group surveys. Particularly noteworthy is his occasional use of genitalic and other characters having positive discriminatory worth, though—with the exception of tarsal segmentation, which was thought to mark a fundamental dichotomy—they were, for the most part, regarded as subsidiary to venation. Other outstanding writers were Banks (1903–1947), Ribaga (1900–1911, Italy), and Navás (1907–1936, Spain). Shipley (1904, England) raised the psocids to ordinal rank when he limited the order Psocoptera to psocids exclusively. Perhaps of equal systematic importance during this period was the demonstration of the unreliability of venation as a basis for classification. Although this was clearly indicated by the divergent views of relationship expressed in the proposed classifications of Enderlein (1903, 1911), Tillyard (1926, New Zealand), Banks (1929) and Karny (1930, Java) the fallacy was not recognized until the second phase of this period.

During this next phase, covering the last thirty years, with the general adoption of alcohol as a preservation medium and the more accessible and improved stereoscopic microscopes, the emphasis has centered on a search for reliable taxonomic characters. Genitalic conformation has been found to be of special value, as indicated by the studies of Chapman (1930), Gurney (1939, 1949), and Sommerman (1942–1948) in this country, and of Ball (1926–1940, Belgium), Pearman (1924–1951, England), Badonnel (1939–1951, France), and Roesler (1935–1944, Germany) abroad. Numerous observations on biology have appeared since the turn of the century and these, along with the genitalic studies, have been used in developing a new framework for classification, founded on general morphology, as outlined by Pearman (1936), then modified and expanded by Roesler (1944). There still remain imperfections at some points. Since 1903 well over three hundred psocid papers have been published, about one-sixth of which are contributions from the United States. At the present time there are about 1,200 described species composing nearly 230 genera in 26 families; of these the United States claims 11 families, comprising 30 genera and 135 species. The main United States collections of native psocids are located at Cambridge, Massachusetts (Museum of Comparative Zoology); Washington, D. C. (U. S. National Museum); Urbana, Illinois (Illinois Natural History Survey); Geneva, New York (Chapman Collection), and Orlando, Florida (Sommerman Collection).

In the future much emphasis will be placed on comparative morphology, biology, and geographic distribution. Careful dissection is an indispensable prerequisite for morphological studies, and progress would be accelerated if a trouble-free permanent mounting medium of low refractive index could be developed for the preservation of reference microscope preparations.

THYSANOPTERA

Stanley F. Bailey
University of California, Davis

Most specialists in the order Thysanoptera recognize as milestones the description of the first thrips by De Geer in 1744 and the proposal of the ordinal name by Haliday in 1836. Linnaeus, Fabricius, Latreille, and Burmeister classified this group of insects with the early hemi-homopteroid or orthopteroid groups. Westwood in 1840 presented one of the first outlines of the order with a summary of its taxonomic evolution. In 1895 Uzel published the first comprehensive review of the order with keys which, together with Hinds' (1902) classic review of the group in North America, stimulated entomologists to take up the group.

Up to this time a bare skeleton of families with scattered genera made up the somewhat shaky taxonomic framework of the order. After the turn of the century the main work of filling in the great gaps was carried by Moulton (1907–1939), Karny (1908–1928), Bagnall (1908–1936), Watson (1913–1946), and the two outstanding living world authorities, Priesner (1914–) and Hood (1908–). The synopses, keys, monographs, and descriptions of hundreds of species of these workers make up the greatest part of the knowledge of Thysanoptera. However, there has been a tendency to create new families and groupings when bizarre, widely separated genera are found. Priesner, in his *Genera Thy-*

sanopterorum (1949) telescopes much of this unnecessary superstructure. Hood in 1915 estimated that about 25,000 forms would be found to exist; to date hardly half that number have been described.

In the modern sense the old carded specimens are impossible to work with or to identify to species. Carefully prepared slide mounts are a necessity and descriptions and drawings prepared from them should be done with the best optical equipment. At present the greatest need for the younger workers is up-to-date illustrated keys to the species.

Geographically, our knowledge of the group is most complete in Europe and in North America. Hood and Moulton have greatly broadened the knowledge of the South America fauna. Priesner has done the same for North Africa, Faure and others in South Africa, Ayyar in India, Kurosawa, Karny, and Priesner in other parts of Asia, Bagnall and Moulton in Australia. In China, equatorial Africa, India, Micronesia, and South America there remain many species yet to be collected and described.

The economic importance of thrips was recognized almost as early as their taxonomic independence. The scarring and blasting of fruits, vegetables, and flowers were described in early gardening guides in Europe about one hundred and fifty years ago. In North America, Fitch (1855) and later Osborn, Pergande, Ashmead, and others described injurious forms, particularly in *Insect Life*. We now know that some species are predaceous, while others are fungus-feeders, gall-formers, and vectors of plant disease (Sakimura, Bagnall, Karny, Hood, etc.).

Our knowledge of the morphology and internal anatomy of thrips has been advanced by the classic studies of Jordan, Klocke, Peterson, Borden, Doeksen, Reyne, Sharga, and Pussard-Radulesco. Extensive studies of the immature forms have been published by Priesner, Karny, Reyne, Melis, and Speyer. Kurdjumov first observed the cocoon-spinning capacity in this transitional order.

The thrips collections of note are the very extensive private collections of H. Priesner, which includes Karny's, and that of J. D. Hood. Museum collections are those of the British Museum, including the Bagnall Collection, U. S. National Museum, California Academy of Sciences (Moulton collection), Canadian National Museum, and Queensland Museum. University and other institutional collections are those at the Illinois Natural History Survey, University of Florida (Watson collection), University of Massachusetts (Hinds collection), and the University of California. Private collections containing much valuable material are those of Faure, Jacot-Guillarmod, and Hartwig of South Africa; those of Williams, Morison, Speyer, Doeksen, Pelikan, and the late Hukkinen, in Europe; those of Sakimura, Bianchi, Kurosawa, and Takahashi in the Orient (little is known of collections in India); and those of André, Steinweden, J. G. Watts, H. E. Cott, and R. L. Post in the United States.

In the future, to bring the order Thysanoptera up to the status of other more completely studied insect groups, it will be necessary for two types of work to continue: the collection and adequate description of new forms and the periodic compilation and evaluation of the accumulated knowledge. In this process the concept of the relative value of family, generic, and specific characters should be refined and better stabilized.

HOMOPTERA AUCHENORHYNCHA

Z. P. Metcalf
University of North Carolina[1]

As I contemplate the literature devoted to the suborder Homoptera Auchenorhyncha on file in my laboratory, I am more and more impressed with the progress that has been made during the last century.

There are in this library about 12,000 different items; all of the books and papers, bulletins and circulars that have been printed about the Homoptera, except fifty, more or less. These fifty, to which I find some reference in the literature, are not to be found in the great American libraries, nor in any of the great European libraries, so far as I can discover. Many of the earlier works are in Latin, and not a few in Chinese and Japanese, which are, as far as I am concerned, knowledge securely locked up. I wish that each of these books and the important papers might pass in review so that the reader might comprehend the history of the science of entomology as it refers to the Homoptera. Here are the great classics of ancient times that tell of the struggle of a beginning science called entomology; also the more recent monographs devoted to single families or even to single genera—the work of a whole host of men deeply interested in our science. What a marvelous tale they have to tell also of far away places and strange faunas! Places about whose people we know very little sometimes contribute the most to our science; the upper reaches of the Congo River, Tanganyika, South Africa, Tibet, Java, Sumatra, Celebes, New Guinea, the great interior of Australia, the high mountains of Peru, Ecuador, the upper reaches of that greatest river basin of them all, the Amazon, with its marvelous fauna.

As I realize that this group has grown, since 1758 when Linneaus described one genus and 42 species, to a group composed of 45 families, about 3,500 genera, and approximately 30,000 species, I am convinced that no one should attempt to understand the suborder as a whole, let alone attempt to describe the progress that has been made over a century of time.

If history is simply the lengthened shadow of the great men who made it, then in discussing the history of a group of insects one must perforce devote most of his time to a discussion of the men who made that history. In a short paper such as this to cover more than the mere outline of the development of the study of the Homoptera is impossible.

When we think of progress in a field of biology we perhaps think first of progress in the field of taxonomy because here we have in the number of genera and species discovered a convenient measure of progress.

For the century beginning with 1850, it is convenient to recognize three periods. Up to about 1850 most of the students of insects were entomologists who studied more than one order of insects. About 1850 the study of entomology began to show a good deal of specialization so that by the beginning of the century 1853–1953 there were a number of students of the group Hemiptera, including both the Heteroptera and the Homoptera.

---

1. North Carolina State College of Agriculture and Engineering.

At the beginning of this century Stål, a great Swedish hemipterist, commenced his work. Perhaps no student of the order Homoptera has had a better grasp of the fundamental groups and the fundamental phylogeny. He was ably assisted by a fairly large group of students of Homoptera in Europe, including Walker and Marshall of England, Signoret of France, and Fieber of Germany. Most of these men had ceased publication by the end of the second decade of the century. In America at this same time the most outstanding student of this order was Fitch in New York.

Walker worked on the extensive collections in the British Museum and described many new genera and numerous new species from all parts of the world. Unfortunately, he did not seem to have a clear concept of taxonomic units. He made numerous mistakes in assigning species to genera, and formerly it was quite the fashion to condemn his work universally; however, recent students in restudying his material have had a better appreciation of his work. Marshall worked on a taxonomic review of the species then known from Great Britain and contributed a sound foundation on which future students of the British fauna could work. Signoret's studies were most extensive in his reviews of the genus then known as *Tettigonia* and related genera, and of the species which he considered closely related to the genus *Acocephalus*. Fitch's catalogue of the specimens in the State Cabinet of Natural History, with careful descriptions of the species known to him, was the foundation for future studies by American homopterists.

After this first period in the development of taxonomy in relation to the Homoptera, the large number of workers as well as their increased specialization makes it difficult to summarize the contributions of each student. I have simply listed these workers, therefore, together with the years during which they made their principal contributions, and will leave it to the individual student to make his own summary.

The next three decades showed a large increase in the number of students who devoted their primary energy to this order. During the first two decades these students devoted their time principally to the larger and more conspicuous species. Beginning about 1870 more emphasis was placed upon the local faunas of the various European countries, and of the United States and Argentina in particular. Some of the outstanding students of this time and the periods of their contributions were the following: Ashmead, 1880–1900; Berg, 1879–1899; Distant, 1878–1920; Edwards, 1877–1928; Horváth, 1871–1931; Lethierry, 1869–1894; Melichar, 1896–1932; Puton, 1869–1899; Scott, 1870–1886.

From 1900 on there has been a great tendency to discuss or to review single genera and their species, usually from a restricted area: Baker, 1895–1927; Ball, 1896–1937; de Bergevin, 1910–1934; Breddin, 1896–1905; Buckton, 1889–1905; Davis, 1885–1942; Fowler, 1894–1909; Funkhouser, 1913–1951; Goding, 1890–1939; Jacobi, 1902–1941; Kirkaldy, 1899–1913; Lallemand, 1910 to date; Matsumura, 1898 to date; Osborn, 1884 to date; Edmund Schmidt, 1904–1937; Swezey, 1903–1942; Van Duzee, 1888–1940.

Since about 1920 more and more studies have appeared on the internal male genitalia as the court of last resort in defining species. Some of the principal workers of this era are the following: Beamer, 1924 to date; China, 1923 to date; De Long, 1916 to date; Esaki, 1922 to date; Evans, 1931 to date; Fennah, 1939 to date; da Fonseca, 1926 to date; Kato, 1925 to date; Kusnetzov, 1925–1938; Lindberg, 1923 to date; Muir, 1906–1934; Nast, 1933 to date; Oman, 1930 to date; Ossiannilsson, 1934 to date.

I have listed above the men who have been chiefly responsible for our present-day concepts of the systematics of the group. Many other students of morphology, phylogeny, fossil insects, physiology, ecology, and especially economic entomology have contributed greatly to our knowledge, but their numbers are so large that it is not possible to evaluate here their contributions.

Our next purpose is to summarize very briefly the developments that have taken place in the study of the Homoptera. Before 1853 most students of entomology devoted themselves almost exclusively to the larger and more conspicuous insects; and the Homoptera, particularly the smaller leafhoppers, planthoppers, and froghoppers, were largely neglected. The larger and more conspicuous singing cicadas and a few of the more conspicuous treehoppers, particularly those from South America, received some attention.

More and more attention, however, has been devoted not only to the smaller Homoptera of Europe and North America in particular but from various parts of the world. It was in this period also that Fieber, studying the smaller European planthoppers of the family Araeopidae, emphasized the importance of a careful study of the details of the male genitalia. Fortunately, in this family there are abundant characters in the external male genitalia for determining most species, and it is not necessary to make elaborate dissections and clear these parts in order to appreciate the importance of these characters.

Unfortunately, however, Fieber's contribution was almost completely neglected for fifty years, while students devoted themselves to the finer and finer details of the external anatomy of the insects of this order and did not study the internal genitalia. Increasing attention was given, for example, to the relative proportion of parts, particularly the length and breadth of the face, of the crown, of the pronotum, of the mesonotum; some attention was paid to wing venation and some to the external characters of the male and female genitalia, particularly the last ventral plate of the female in the leafhoppers and the proportions of the valve in the male. But beginning about 1920 students of Homoptera placed increasing emphasis on the details of the various structures revealed by careful dissection and clearing of the male genitalia. In this connection one may point out that perhaps too much emphasis has been placed upon the fine details of the aedeagus. Subsequent studies may show, however, that even greater emphasis is needed on the study of this structure and that what we now consider good genital characters for the differentiation of species are of generic, not specific, value. On the other hand, perhaps too little emphasis has been placed upon the general picture of the male and female genitalia as generic characters. And I believe that one of the developments for the future will be in this particular area.

In other areas, however, the study of the Homoptera has not kept pace with the development of taxonomic studies. Fairly comprehensive studies have been made in the general morphology of the head, of the wings, and of the male genitalia. Still more detailed work needs to be done in all of these areas and particularly in the morphology of the thoracic sclerites before we have a comprehensive view of the morphology of this interesting group of insects.

Other morphological structures have been greatly neglected. The internal morphology of a few of the larger species has been studied, but more careful studies of the internal morphology of many of the smaller species are needed. I feel safe in saying that we do not have sufficient knowledge of the morphology of enough representatives of the various families, tribes, and subtribes to generalize about the phylogeny of the group as a whole.

The study of the physiology of the Homoptera has been woefully neglected. We have perhaps a beginning of comprehension of their methods of feeding, and a little knowledge about their digestion, especially in some of the vectors of plant diseases. A startling discovery by Ossiannilsson that all these insects, and not the cicadas alone, are singing insects, is perhaps one of the most interesting developments. Except some minor contributions on the secretion of wax, honeydew, the formation of froth in the froghoppers or spittlebugs, there is little of real importance in the study of the physiology of these insects. The study of many other physiological aspects awaits better techniques than any now available, especially for the investigation of the smaller forms.

In the field of ecology most of the contributions have been on the food plants of the various species. One would gather the impression that these insects were almost exclusively confined to a single host plant or to a very limited order of host plants, and that only a few species are rather general feeders. My own impression from limited study would lead me to believe that the exact opposite may be true and that the limiting factor is perhaps the sum total of all the physical and biological features of the environment. Thus a species, if it finds other favorable physical and biological factors, may transfer its attention from one host plant to another belonging perhaps to an entirely different group of plants. Now such an assertion as this is exceedingly difficult to prove because, in the first place, we cannot at present be even reasonably sure what the physical or biological factors in the environment are or what is the insect's ability to adapt itself to their extreme ranges. Neither can we be sure that we know the most important physical and biological factors in the environment of these insects. We assume that temperature, humidity, and food plants rate very high, but we have very little evidence of their importance.

As illustrations of these two points I have only to report three limited observations. What is apparently the same species of small planthopper was described originally from *Spartina* grass growing on the high dunes of Long Island, and has been taken also on a species of *Uniola* growing on the high dunes along the North Carolina coast. Here we have, apparently, two different regions with approximately the same physical factors harboring the same species of insect. In Northern Michigan, however, I observed another larger species of planthopper living in the sheltered beach pools on rushes, whereas this planthopper was not found along the shores of the lake where the rushes were subject to high winds. Every student of this order who has collected extensively in the field has had this experience. Two nitches, which are as far as can be judged identical in the more important biological and physical factors, are vastly different in regard to the total population of Homoptera; for the one will yield a large number of specimens whereas the other seems to have none. What then are the factors that make such conspicuous differences? Whether any of these observations will stand the test of carefully planned experiments with accurate measurements of all of the known factors in the different environments should command the study of future students.

That the field of ecology has been too much neglected is abundantly evidenced. I need point out only a single example. Our studies of the great grassy plains of the Missouri and Mississippi valleys have largely neglected the leafhoppers and planthoppers which occur in a normal grasslands area. Yet Osborn's studies showed many years ago that the total population of these insects is of the order of one to two million individuals per acre. Now such an important observation as that cannot be neglected in studying the sum total of all of the factors, physical and biological, in the environment.

There is great need for more careful studies in ecology from all parts of the world. The inference of such studies on the development of the science of ecology and of the economic control of insect pests is incalculable. Careful studies such as are now being made by two Finnish homopterists, Lindberg and Nuorteva, should be initiated by students in all parts of the world.

Until about fifty years ago very little attention was given to the economic importance of the Homoptera. However, a few species received some notice; chief attention was given to the spectacular appearance of the seventeen-year and the thirteen-year cicadas and little attention to the conspicuous but relatively inconsequential damage done by the so-called buffalo treehopper. But starting about fifty years ago a sequence of events impressed upon entomologists the importance of the Homoptera in relation to crop damage. One of the earliest and most spectacular of these incidents was the great destruction wrought to the sugarcane fields of Hawaii by the sugarcane planthopper imported from Australia or New Guinea and its control by introduced parasites. Also relatively early was the damage caused by the sugarcane froghopper in Trinidad. Following this was the destruction by the potato leafhopper of potatoes, beans, and peanuts, and the damage caused by the sugarbeet leafhopper to the growing of sugarbeets in the western United States. More recently, the damage caused by the alfalfa froghopper has again emphasized the importance of these insects as pests of agricultural crops.

Concurrently with the foregoing, or nearly so, there developed the appreciation of the economic importance of these insects, particularly the apple leafhopper complex; various species of cotton leafhoppers in Africa, India, and Australia; the importance of the grape leafhopper in the United States; of leafhoppers on cranberries in New Jersey; and of leafhoppers and planthoppers on rice, particularly in Japan. Other economic pests perhaps should be mentioned, but most of these are pests of minor crops or are of only local consideration at present.

Another development is the importance of these insects as vectors of certain diseases of crop plants. Recent important summaries of these have been published, and mention should be made of such important diseases as curly-top of sugarbeets and other types of curly-top transmitted by *Circulifer tenellus,* of peach yellows by *Macropsis trimaculata,* of the phloem necrosis of the elm by *Scaphoideus,* and of various mosaic diseases and several kinds of yellows transmitted by leafhoppers.

The life histories of many of the economic pests belonging especially to the leafhopper group have been studied but there are many other forms which have received only cursory attention. The life history of the seventeen- and thirteen-year cicadas in North America is well known owing to the comprehensive studies of Marlatt. Osborn and Ball made very great contributions to the life histories of the leafhoppers in Iowa many years ago, and Osborn studied the life histories of the leafhoppers of Maine and the froghoppers of the same region. More recently some contributions have been made to the life history of the alfalfa froghopper. Some general studies of the life histories of the treehoppers were made many years ago by Funkhouser, and some of the economic pests in this group have been rather generally studied. Much still remains to be done, especially in the tropical regions of the world. The fulgorids have been rather generally neglected; the life histories of only a few species have been studied and these rather incompletely.

The phylogeny of the group as a whole is rather poorly understood. Most of our present-day discussions are based upon the studies of Stål, made nearly 100 years ago. Less than 500 of the present known 3,500 genera and perhaps less than 4,500 species of the known 30,000 species were then known. Stål conceived the group as comprising four families and for the most part we now consider these of superfamily or even higher rank. Basing our studies of the group's phylogeny on such a small area of the total population would be like basing our studies of geography on the knowledge of geographers of the world before the discovery of America by Columbus, or basing our studies of history on only the history known before the beginning of the Christian era.

Fairly comprehensive studies of the genera of Fulgoridae by Muir and others, of the Cercopidae by Lallemand, of the jassids by Evans, Oman, and others, and of the Membracidae by Funkhouser give a rather firm basis for comprehensive study of the phylogeny of these groups. Perhaps what is most needed now is research on the phylogeny of the families and of the groups higher than the families. For the present I believe that the knowledge of the subfamilies, perhaps of the tribes, of most of the groups is fairly comprehensive.

What, then, of the future? What the future holds for the field of taxonomy is anybody's guess. Whether other characters will influence the taxonomy of the group as profoundly as the discovery of the importance of male genitalia has influenced it in the last quarter century remains unknown. Yet I believe that other characters quite as important as the morphology of the male genitalia will be discovered in the not too far distant future.

The present tendency is to confine taxonomic studies to a single genus restricted to a limited area of the world's surface. Perhaps this is the best method for making progress. It is unfortunate, however, that so few students are sufficiently interested in the suborder as a whole to devote their time and attention to the groups higher than genera. Very little progress in taxonomy is going to be made until we have a thorough restudy of at least the external morphology of these interesting insects, correlated perhaps with a study of the internal morphology, of physiology, embryology, ecology, and zoogeography. This, indeed, sounds like a comprehensive program but as long as our knowledge of taxonomy is based upon the phylogenetic concepts of Stål of one hundred years ago and as long as we confine the insects of this group to four or five families, just so long will our taxonomic concepts be inadequate, for the consideration not only of the species already described, but of the genera and species not yet described.

We hear on all sides complaints about the rapidly changing nomenclature, and the International Commission is engaged apparently in an attempt to stabilize our nomenclature by decrees fixing certain names. How futile this is can be appreciated from a number of apparent facts. First, it is doubtful whether we know more than a third of the genera and species of the Homoptera Auchenorhyncha now living in the world. Second, until recently we have had no comprehensive bibliography of this group. Third, only about a fifth of the families have been covered with an up-to-date catalogue of the genera and species. It might be remarked in passing that although I spend a considerable portion of my time on the current literature, I can just barely keep pace with it. Yet I am foolhardy enough to believe that any attempt to fix names is going to fail utterly; first, because there are not enough workers to study all of the literature of the past and to fix names with accuracy, and second, because the names that are fixed are bound to change with our increased knowledge of the real taxonomy of the group.

The changes in nomenclature in systematic zoology are no more drastic than the changes in the nomenclature of any other science, biological or physical, which is developing rapidly. There is something amusing, if not ridiculous, in reading biological papers and noting how carefully the writer has checked every factor involved except the accepted nomenclature of the day.

If evolution is an explanation of the facts of the biological world, then the center of origin theory must be accepted. That is, there must be for each species and each genus a center on the earth's surface where these units of the animal kingdom have arisen. It follows, therefore, that a clear understanding of the zoogeography of the animals of a group is a necessary prerequisite to an understanding of the taxonomy, ecology, phylogeny, and other areas of the field of biology. A great deal of progress has been made in the study of the zoogeography of the Homoptera. Of course, much more than has already been discovered awaits the inquiring mind of the future student. Most of the facts of zoogeography are so patent that they would seem to need little argument for their support. Except where nature has been interfered with by man and his commerce, we would naturally expect that species would spread from their center of origin gradually, perhaps more rapidly than we think, to other areas to which they can adapt themselves. A firm foundation for our study of zoogeography was established by many different workers working on local lists of the countries of Europe, the states in the United States, South Africa, India, Japan, Australia, various countries in South America, and other regions.

The real purpose of a short history such as this is to call attention to the great areas of study which await the nimble fingers and keen minds of future research workers. For these alone can develop the techniques which will push forward the frontiers of our knowledge of one of the larger orders of the insect kingdom and one which contains some of the most bizarre animals known to man.

HEMIPTERA

Robert L. Usinger
University of California, Berkeley

The status of our knowledge of the Hemiptera in 1853 can be summarized by citing the best general work of that period, Amyot and Serville, *Histoire naturelle des insectes, Hémiptères* (1843). This classical work was built upon the solid foundations of Linnaeus (1758, 1763), Fabricius, especially the *Systema Rhyngotorum* (1803), Latrielle (1796–1810), Dufour (1833), Burmeister (1835), and Westwood (1840). In the United States, Thomas Say (1831–1832) should also be mentioned with this group of pioneers. In 1853 no general catalogue existed, but at the end of the decade Anton Dohrn (1859) published his *Catalogus Hemipterorum.* This was the first world catalogue of this great order.

Since 1853 tremendous progress has been made. Perhaps the greatest single step was the work of the Swedish father of hemipterology, Carl Stål. Stål was the greatest hemipterist of all time and managed to crowd into his brief forty-five years of life the publication of fundamental works in the Orthoptera, Chrysomelidae, and Hemiptera. Stål had a remarkable sense of fundamental characters and his keys to the principal groups of Hemiptera are still the best keys we have in certain groups. His epoch-making *Enumeratio Hemipterorum* (1870–1876) in five parts has been called the hemipterist's bible. Unfortunately this great work did not include a treatment of the difficult and very large family Miridae.

Following upon the work of Stål another Scandinavian, O. M. Reuter, developed a classification of the Miridae which filled the great gap in Stål's work. Reuter devoted himself in the later years of his life to a fundamental phylogenetic study of the Hemiptera (1910, 1912). China and Meyers (1929) contributed further to our knowledge of phylogeny and still later (1933) China gave the latest phylogenetic diagram.

Greatly augmenting our knowledge of the Hemiptera of foreign places, the great faunal works appeared during the last half of the nineteenth century. Among these may be mentioned the *Fauna of British India* by Distant and the *Biologia Centralia-Americana* and the *Fauna Hawaiiensis.* These and other great works expanded our knowledge to all parts of the world and gave a breadth to the classification of the Hemiptera that was not present before this time.

Cataloguers were very helpful in the latter part of the nineteenth century, and especially to be mentioned is the great *Catalogue général des Hémiptères, Hétéroptères* (1893–1896) by Lethierry and Severin. The Lethierry and Severin *Catalogue* is still the only world catalogue for most groups of Hemiptera. Unfortunately it did not include the Miridae nor the aquatic Hemiptera. Atkinson gave us the *Catalogue of the Capsidae (Miridae)* (1889), and this is still our best catalogue for this important family. Only recently, starting in 1927, was an attempt made to prepare a new *General Catalogue of the Hemiptera.* This enterprise was a cooperative one with contributions from scientists throughout the world. A number of fascicles appeared over a period of twenty years. The enterprise was abandoned recently by Smith College, but has been revived by Z. P. Metcalf at North Carolina State College.

The growth of collections marks the development of most of the systematic sciences and this is true in hemipterology as well. The great collections of the present time are the collections of the British Museum (Natural History) in London, the Naturhistoriska Riksmuseum in Stockholm, and the great museums in Helsinki, Vienna, Berlin, Paris, Budapest, Leyden, Genoa, and to a lesser extent elsewhere on the European continent. In the United States great collections were developed somewhat later, and among these may be mentioned those of the United States National Museum, the Museum of Comparative Zoology, the American Museum of Natural History, the Academy of Natural Sciences at Philadelphia, the California Academy of Sciences, the Carnegie Museum, the Chicago Natural History Museum, the Museum at Cornell University, the Snow Museum at the University of Kansas, the Museum at the University of Michigan.

Progress in the classification of Hemiptera may be marked not only by the traditional taxonomic works but also by great landmarks in improved approaches to the subject. One of these was the publication by Singh Pruthi on male genitalia in the Hemiptera. This work was published in 1925 and provided a new set of data upon which to base classifications. Another new set of characters was discovered by Tullgren (1918) and Ekblom (1928). These authors found the maxillary levers to be of significance in the higher classification of the Hemiptera, and also found that the arrangement and position of the trichobothria were of significance in the over-all classification.

During the period of taxonomic progress, other students were furthering our knowledge of the biology of the Hemiptera. Among these the first was Dufour (1883). Later Hungerford, Hoffman, Miller, Readio, Butler, and Weber contributed greatly to this field. The subject of the physiology of insects was also pursued during much of the period covered by this century. Dufour (1833) did the first significant work in this field but classical studies awaited the researches of Wigglesworth. Wigglesworth selected as his experimental animal the bug *Rhodnius prolixus*. *Rhodnius*, being a blood-sucking insect, was especially well adapted to studies of this kind because it could be reared in the laboratory and fed only once between each instar. Wigglesworth studied the moulting of insects and many other details of the physiology of insects.

The subject of genetics should be mentioned because bugs were used very early in the development of this science. The Pentatomids, in particular, were used for cytological studies in the early part of the present century. Recent work of this kind is much more far-reaching and concerns the chromosomes of many other families of Hemiptera. It is too early to say what significance this work may have on our final classification, but certainly karyology will provide an additional set of taxonomic characters.

Economic investigations have always played an important part in entomology, but this has come to be more striking during the twentieth century. In the Hemiptera the most important pests are the bedbug, which was studied from earliest times; the chinch bug, which is so injurious to agriculture in the Middle West and was one of the earliest insects of economic importance to be studied in the United States; lygus bugs, which have come to the fore only in the last few years. Among the numerous other pests are the squash bug and the harlequin cabbage bug. Of great importance in biological control in the 1920's was a bug of the genus *Cyrtorhinus*. This bug had the remarkable property of sucking the eggs of leafhoppers and was therefore introduced into the Hawaiian Islands to control the sugarcane leafhopper. It is now a matter of historical record that *Cyrtorhinus mundulus* brought the sugarcane leafhopper under control and saved the sugar industry for Hawaii.

Another important group of hemipterous insects is the subfamily Triatominae. Triatoma bugs are the vectors of the American trypanosomiasis or Chagas' disease. This disease of tropical America was discovered in 1909 by Chagas and since that time many investigators have contributed to our knowledge of the disease and its control.

The modern period in systematic studies of the Hemiptera in the United States was inaugurated by Uhler in the latter part of the nineteenth century. It was carried on by Van Duzee, Barber, Blatchley, Heidemann, Drake, Knight, Harris, Fracker, McAtee and Malloch, Hungerford, Hussey, Parshley, Torre-Bueno, Sailer, and by a host of others. Elsewhere in the world outstanding work was developed by Horváth, Schouteden, Poppius, Kirkaldy, Bergroth, Handlirsch, Wagner, Lent, Kormilev, De Carlo, Hoberlandt, Blöte, Carvalho, Brown, Bruner, Costa Lima, Jaczewski, Lundblad, Mancini, and many others.

It is difficult to anticipate trends, but a look into the future may not be out of keeping at this point. At the present time it may be said that most of the regions of the world have been explored fairly adequately, but that our fundamental classification, the phylogenetic scheme for the Hemiptera, is still not entirely satisfactory. The basic division into Gymnocerata and Cryptocerata, based upon whether or not the antennae are concealed, is quite artificial. Therefore, we need a comprehensive phylogenetic study of the entire order and this will undoubtedly develop out of work that is now in progress in various parts of the world. Second, we need a collation of the regional works that have been pursued by students in various museums in various parts of the world. At the present time it is possible to go from one European museum to another, or from an American museum to a European museum and find type specimens standing under different names in each museum. The fact is that no one has systematically compared these types and established the synonymy which is so necessary before any really comprehensible classification can be established. Finally, we need a modern catalogue of species and keys to the genera of Hemiptera for the world. Thus it might be said that the analytical part of Hemiptera classification has been fairly well done but that the synthetic part—the bringing together of all the information—remains to be done. Therefore it is clear that the next century has a big, and perhaps the most significant, task ahead, namely, to bring all of the scattered information together into a comprehensible whole.

NEUROPTERA AND MECOPTERA

F. M. Carpenter
Harvard University

By 1853 the Neuroptera and Mecoptera were being investigated by a number of well known entomologists. F. Brauer had published more than a dozen papers on them, mostly dealing with life histories, and L. Dufour had made important contributions to a knowledge of their internal structure. Taxonomic studies were being carried on by H. Burmeister, J. Curtis, J. O. Westwood, F. Walker, P. Rambur, and H. Hagen. At that time, of course, the order Neuroptera was an ill-defined assemblage of unrelated insects, including mayflies, dragonflies, termites, bark lice, stoneflies, and scorpion flies, in addition to the insects now termed Neuroptera. Just a century ago E. Newman, following a suggestion made earlier by Erichson, proposed a division of the order. One group (Neuroptera) was to include the insects which we now know as Neuroptera, Mecoptera, and Trichoptera; the other (Pseudoneuroptera) was to contain all the other families previously placed in the order. Although further limitation of the order Neuroptera has since been made, Erichson's and Newman's proposals were significant in two respects: they emphasized the difference in the metamorphosis of the two groups of insects thus separated and they anticipated the natural or phylogenetic classification of insects which was more generally applied several years later, following publication of the *Origin of Species*.

The order Neuroptera of Erichson and Newman was usually subdivided by contemporary entomologists into four families: Sialina, Hemerobina, Panorpina, and Phryganina. Ordinal separation of the caddis flies and scorpion flies was gradually made in publications by C. Gerstaecker (1863), C. Gegenbaur (1877), F. Brauer (1885), and N. Banks (1892).

From 1850 to 1890 there were only three major workers on Neuroptera and Mecoptera. Brauer continued his studies on their life histories and immature stages, dealing chiefly with Austrian species. Hagen published many taxonomic and biological papers, especially on New World species, his *Synopsis of the Neuroptera of North America, With a List of South American Species* being the most comprehensive treatment of the group which had appeared up to that time (1886). R. MacLachlan, also, made many important contributions to the knowledge of the world fauna, including a revision of Walker's *British Museum Catalogue of Neuroptera* and a monograph of the British Neuroptera.

Since 1890 there have been many more workers on Neuroptera and Mecoptera. Nathan Bank's published works, beginning in 1892, is the most extensive and on the widest geographical range of material. H. W. van der Weele has also contributed numerous works on species from many parts of the world, his revisional studies (Ascalaphidae and Megaloptera) being especially important. In more recent years D. E. Kimmins has published numerous papers dealing with the faunas of all zoogeographic regions. L. Navás has described a great many species and L. Krüger numerous genera, both inadequately and on insufficient material. K. J. Morton, Bo Tjeder, J. L. Lacroix, J. A. Lestage, and P. Esben-Petersen have restricted their studies largely to Old World species, though Esben-Petersen's monographic revision of the Mecoptera (1921) covered all species known at the time. F. J. Killington, whose *British Neuroptera* (1936–1938) is truly a classic in the literature on this group, has dealt mainly with British species. Similarly F. Klapálek has published studies chiefly on European Neuroptera and Mecoptera; R. J. Tillyard on the Australian fauna; R. Smith and F. M. Carpenter on the Nearctic members; and Issiki, Miyake, Nakahara, and Okamoto on Asiatic species.

Much of the revisional work done in recent years has been based on detailed structure of the terminal abdominal segments. Studies of this kind, involving reworking of type material, have cleared up much of the confusion that has attended the taxonomy of both Neuroptera and Mecoptera in North America and Europe, but continuation of such investigations is still the prime need. Basic and extensive study collections of Neuroptera and Mecoptera are contained in the British Museum (Natural History), which includes the Walker and MacLachlan collections (among others), and in the Museum of Comparative Zoology, Harvard University, which contains the Hagen and Banks material. Other large museums, of course, also have important study collections, but of more recent origin.

Another need, just as important, is studies on the life histories and immature stages of these two orders of insects. Virtually only the British and certain European species are satisfactorily known.

TRICHOPTERA

Herbert H. Ross
Illinois Natural History Survey, Urbana

If the starting point of this discussion had been set two years earlier, it could honestly have been said that caddis flies in North America were then represented by only a handful of scattered descriptions. But in 1852[1] F. M. Walker described about 60 species from North America, and this was followed in rapid succession by additional descriptive efforts by Hermann Hagen, Kolenati, and the Abbé Provancher, so that by 1880 some 150 species were described from the North American region.

Even with the inclusion of Walker's work there was relatively little known about North American Trichoptera in 1852. Only a few species described by Thomas Say had been illustrated in American scientific literature, while the other species were known only by brief, inadequate descriptions. The European fauna, however, was surprisingly well investigated. Especially notable had been the researches and publications of the Swiss worker, Pictet. In 1834 he gave a fine account of the main groups of the European Trichoptera, illustrating not only many pertinent features of the adults and larvae, but also life-history data on most of the large groups. Pictet divided the Trichoptera into about ten genera, and these anticipated in almost uncanny fashion the major groupings which later became established in the order. Contemporaneously with Pictet, two British workers, Curtis and Stephens, made significant contributions to the recognition of caddis-fly genera, and Zetterstedt added considerably to the knowledge of the fauna of northern Europe. Up to this time, however, the generic and specific diagnoses were on a very superficial level, and information was available in usable form for only a few sections of the European fauna.

---

1. Here and elsewhere in this article, dates refer only to publications, for which the full references may be found either in Bull. 292, New York State Museum, or in *Zoological Record*.

The modern pattern of caddis-fly study was initiated suddenly and decisively by the English worker, Robert McLachlan, in his monumental treatise on the European caddis-fly fauna (1874–1884). McLachlan defined most of the modern families and genera, introduced genitalic structures as the chief basis of specific diagnosis, and gave a comprehensive set of clear descriptions and illustrations for most of the European species and many of the Asiatic ones as well.

McLachlan's work served as a stimulus to a group of energetic students of the order who described species from every part of the globe. Nathan Banks (1892 to 1951) was especially active in investigating North American, South American, and Pacific Island forms; A. B. Martynov (1892–1934) described much of the Asiatic and Oriental fauna, with especially valuable papers on the Siberian forms; George Ulmer (1900 to date) not only studied the Oriental, Neotropical, and African faunas but also wrote the Trichoptera volume (1907) of *Genera Insectorum*, which has been and still is the starting point of all serious world studies in the order; Longinos Navás (1905–1933), probably the most prolific writer, described material from all areas; and Martin E. Mosely (1919–1948), whose many papers are ably and fully illustrated by D. E. Kimmins, elucidated the Trichoptera of many lands.

Soon after the turn of the century the tremendous upsurge of interest in limnological work added its impetus to caddis-fly studies, especially in the investigations of immature stages. In this field outstanding contributions were made in Europe by Thieneman (1903–1926), Siltala (1900–1908), Wesenberg-Lund (1908–1915), and Ulmer, whose Trichoptera volume (1909) of Brauer's *Susswasserfauna Deutschlands* was of great value for diagnosis. In North America similar studies were reported by Vorhies (1905–1913), Lloyd (1915–1921), and Krafka (1915–1926).

A great boon to taxonomic work on the adults was the discovery late in the last century of the clearing or eviscerating action of sodium and potassium hydroxide solutions. This treatment is especially effective in studying the genitalic structures of insects. One of the first champions of this procedure in Trichoptera studies was Cornelius Betten (1901 to date). Dr. Betten not only instructed many students in the techniques of trichopterology, but gave North America its finest reference book on the order, his *Trichoptera of New York State*, published in 1934 as Bulletin 292 of the New York State Museum.

Many other workers have been attracted to the order in the last few decades, and these have added the results of their work to the total. In North America the more active have been L. J. Milne, D. G. Denning, and the author. In Europe D. E. Kimmins, F. Schmid, and F. C. H. Fischer are especially active in the group.

Looking over the record, we see that our knowledge of the world fauna has increased from the dozen or so species described in Linnaeus' time to the four or five thousand known today. The list of the North American fauna has grown from eight or nine in Say's time to eight or nine hundred described today. Immature stages are known for a surprising proportion of the genera (70 per cent in North America). Integration of larval and adult characters has aided tremendously in clarifying concepts of classification.

Trichoptera is a relatively easy order in which to start studies. There are synoptic treatments available for the faunas of several large areas—Europe (McLachlan, 1874–1884), Russia and Siberia (Martynov, 1934), South Africa (Barnard, 1934, 1940), India (Martynov, 1935, 1936; and Mosely, 1933–1949), Sunda Islands and the Philippines (Ulmer, 1930, 1951), eastern and central North America (Betten, 1934; Ross, 1944), and Australia and New Zealand (Mosely and Kimmins, 1952). Many species of other areas are well diagnosed. The excellence of the literature is a real tribute to the high standards of description and illustration set by the pioneer workers in the group.

Three areas of future study beckon the student of Trichoptera. First is the recognition of the many species yet unknown, requiring study of accumulated material and additional collecting in poorly known areas. Second is the need for understanding the identification characters and physiological requirements of larvae, so that these may be used as index organisms and possibly as habitat conditioners in the control of pollution and in fish management. And third, there is the need to integrate all this on a world basis, so that we may learn more about the evolution and dispersal pattern of the Trichoptera and apply these findings to the solution of some of the many vexing problems confronting the evolutionist and ecologist.

LEPIDOPTERA

William T. M. Forbes
Cornell University

Like most things in the fields of philosophy and science, the serious study of the Lepidoptera starts with Aristotle, who used the cabbage butterfly and the native silkworm (probably *Saturnia pyri* or *Pachypasa otus*) as examples of metamorphosis. If we may judge by Pliny, his classical followers added little in fact and nothing in method, and the revival of science after a millenium and a half produced quite a little new factual material, but showed little improvement in the casual method of presentation used by such workers as Redi and Aldrovandi, Swammerdam and Leeuwenhoek, Mouffet, and even Petiver.

Mme. Merian's little book of fifty plates, with a short text, on an equal number of Lepidoptera with their caterpillars and a word on their biology, makes a step forward in the orderly presentation of the group, and this was soon followed (1679, 1683, 1718) by a hundred more, giving for the first time a unified picture of the order for any region. In the same period (1705) she also opened the tropical Lepidoptera to our view including the larvae, with sixty plates, from Surinam.[1]

The next high spot is the sixth edition of Linnaeus' *Systema Naturae*, in which he tries out his new binomial system on nearly forty Lepidoptera selected

1. I do not cite the exact titles of these two works, for they differ in the German, Dutch, Latin, and French editions; they can be found in Hagen's *Bibliotheca*, Horn and Schlenkling, or Stuldreher-Nienhuis' biography of Mme. Merian.

from his *Fauna Suecica,* as well as in a few other groups of animals. I very much doubt if the experiment looked as important at the time as it turned out to be. Almost contemporary is Lyonet's *Traité Anatomique de la Chenille* (1760), so thorough a piece of work that, when I dissected the muscular system of the tent caterpillar I found this publication more accurate than any later work; and when Williams rediscovered the prothoracic endocrine gland of the caterpillar, he found it already figured and discussed by Lyonet!

Then came the great period of the picture books, adding up to a pretty clear view of the Lepidoptera of the world. Hübner's great series on the European Lepidoptera approached completeness in the butterflies and larger moths, and gave a well-balanced view of the micros. Also, his *Geschichte* is the basis of our real knowledge of the European caterpillars, and his beautiful figures have been copied and recopied right up to modern times. For the exotics nothing remotely resembling completeness was then available, but there were good recognizable figures of all the larger forms from every part of the world, chiefly through the work of Cramer (continued by Stoll) and the publications by Hübner, with Geyer and then Herrich-Schaeffer, and the appearance of many lesser but still important series, continuing into the century of our present interest. Less pretentious in appearance than these illustrated series, but far more scientific in purpose and intended completeness was the French *Encyclopédie méthodique,* beginning with a massive introduction in 1789 and treating (1790–1824) every genus and apparently every known species of Lepidoptera from *Alucita* to *Papilio.* It then broke down, with descriptions of relatively few species of *Phalaena*[2] and the remaining genera; but the butterflies (*"Papillon"*) occupy a whole volume. The publication by Smith and Boisduval of a number of Abbot's drawings, gave the first clear view of the North American caterpillars, and this was supplemented by less pretentious accounts (primarily of economic species) by Peck, Harris, and others.

The last major event before 1853 was the publication of Doubleday's *Genera of Diurnal Lepidoptera* (1846–1852). This work put the classification of the true butterflies on such a solid basis that the major part of it stands to this day. The skippers have needed more drastic revision—and they really still need it.

For the century 1853–1953 we may profitably divide our review into fields of study.

Taxonomy

The field of taxonomy naturally divides into discovery of kinds, cataloguing, and scientific classification.

In 1853 several major works, particularly on the moths, were going through the press. Doubleday's *Genera of Butterflies* had included a complete catalogue; but Walker was working on his *"List"* of the moths for the British Museum, which included short descriptions as well as bibliography, and is in fact the last review of the world fauna to be completed. Guenée was working on the moths on a rather more generous scale for the *Suites à Buffon,* but of this only a few families were completed, essentially the Noctuidae, Geometridae (Phalénites), and Pyralididae. There has been no complete revision of these three families since,

2. Note that in the *Encyclopédie*, as in every following publication for nearly a century, Phalaena, if used at all, meant the geometers, not the noctuids.

though Boisduval's contributions to the same series of the Papilionidae, Pieridae, and Sphingidae are superseded. Herrich-Schaeffer's works were coming out in the same period and supplied figures for many species. The three authors referred more or less to each other, and in some cases no ordinary mortal can tell which author should get credit for a given name, or which is the prior name for a particular species. In the field of major classification each author has a place, but Herrich-Schaeffer, with his more orderly tabulations and keys, has had more influence on later work. Guenée was frequently inspired, but his presentation is less clear, and his attempts to use larvae and biology for classification were often unsuccessful. Walker was too hurried, and most later workers have found it not worth the trouble to dig out the useful elements of his groupings.

This was also the moment at which California appears on the map for Lepidoptera; for Lorquin went out there in the famous year 1849. By 1852 he had turned back from gold mining to entomology and was sending material to Boisduval in France. He ranged from Oregon and the Apache country to "Los Angelos en Sonora," and the results appeared chiefly in Boisduval's two *Lépidoptères de la Californie* and the "Extrait d'une lettre de M. Lorquin sur la faune de la Californie" (*Bull. Entom. Soc. France,* 1856, p. 98). The noctuids, geometers, and pyralids were turned over to Guenée for the *Suites à Buffon.*

The rest of the half-century was a great period for collecting and describing in all parts of this country, till by 1900 we had a pretty good idea of the North American macros. It is not possible even to list the names—in the East there must have been a hundred workers who made real contributions, in the Rocky Mountain area Snow possibly stood above the others, in Texas Belfrage, on the West Coast Hy Edwards. To me, personally, the outstanding figure was F. G. Sanborn, whose collection, much faded by thirty years of exhibition but still intact, was my first introduction to a real collection of moths.

The material collected at this time was worked up by a series of persons, many of them more or less specialists. The bible for the butterflies, sphinges, and bombyces for much of the period was Morris' *Synopsis of the Lepidoptera of North America,* published by the Smithsonian Institution in 1862. It was intended to follow this with studies of the other groups, but only the Geometridae (still "Phalaenidae"), by Packard, actually got published, by the United States Geological Survey in 1876. Packard also continued to work on the "Bombyces," and the Notodontidae, Saturniidae, and Citheroniidae, including most of the caterpillars, were finally published by the National Academy of Sciences in very luxurious form. The rest of the plan, however, disintegrated. The Noctuidae eventually fell to Smith when he came to work at the United States National Museum, and quite a few fragments were published, mostly after the end of the century; while the micros, which were Fernald's portion, were represented by the crambids and pterophorids, published by the State of Massachusetts, and by a bibliographic catalogue of the Tortricidae, which appeared in the *Transactions* for 1882.

This was the period when the butterflies became a major specialty. In addition to innumerable scattered papers, the principal manuals were by Morris, his *Synopsis,* already mentioned, by French and others, culminating in the great works of W. H. Edwards (1868–1884) and Scudder (1889), with their rich illustration and vast data on early stages, Edwards mainly on the western, Scudder only on the eastern species. Holland's *Butterfly Book* (1898) started a new era, for it first figured practically all the butterflies, for both East and West, and at a price the public could easily pay. (It also started the present writer on the Lepidoptera.) In the present half-century local butterfly books have continued to appear. J. H. Comstock's *How to Know the Butterflies* (1904) was more complete on early stages and more compact than Holland, but served for the East only. On the West Coast Wright (1905) would probably have replaced Holland, if the earthquake of 1906 had not destroyed most of the edition. It was perhaps less critical than Holland, but more richly illustrated, and is our chief record of identifications current on the Coast before the fire. For instance, his figures of *Pamphila ruricola,* and J. A. Comstock's figures can be reconciled with the original description, whereas the supposed type and more recent identifications (e.g., of the brown *Atrytone vestris*) cannot.

In the most recent period J. A. Comstock's *Butterflies of California* and Klots' *Field Guide to the Butterflies* will probably dominate their respective areas.

In more scientific classification rather than the discovery and identification of species, another series of authors and works have dominated the field. Here two works stand above the others, even from a world point of view: Doubleday's *Genera* for the first clear picture of the world classification as a whole, and Scudder's *Butterflies of Eastern North America* for the only integration of characters of all stages. Except in the skippers and special studies of limited groups the only other work worth mentioning is Schatz's *Exotische Schmetterlinge: Familien und Gattungen der Tagfalter* (1892), which is roughly the generic part of Doubleday, revised, extended, and brought up to its date. At that time the genitalic and larval characters had not been properly studied for the definition of genera and higher groups, and the time is now more than ripe for another Doubleday or Schatz. Schatz died in the midst of his work, and the classification of the Lycaenidae by Röber represents a lower level of quality.

The major classification of the skippers has had a separate history. Doubleday did little with them, Schatz and Röber omitted them, and their serious study practically begins with Scudder. Druce, in the *Biologia* (1893–1901), and Watson (1893) extended the scientific approach to a world point of view. More recently Lindsey, Bell, and Williams have given us an integrated picture for the United States (Denison Univ. Bull. Journ. Sci. Labor., Vol. 26, 1931). But Evans' World Revision will be the definitive work: the Africans were published in 1937, Eurasians and Australians in 1949, Americans are beginning to appear, and we hope the rest is in press. All the critical work on skippers has included the genitalia, starting with Scudder and Burgess in 1870; but knowledge of early stages has been too fragmentary for any one to go much farther than Scudder did.

Outside the United States the chief region where the butterflies are a special study has been England, I suppose because only in English are there distinctive words for "moth" and "butterfly." Here the works are far beyond counting; I might only mention that I turn most often to South's *Butterflies of the British Isles.*

Classification below the species has gone farthest also in the butterflies. Here we have had a rather violent change in point of view. In the first half of our century most workers who went below the species were chiefly interested in biologically significant or striking variations, and most of the proposed varietal names represented seasonal or dimorphic forms, or even pure aberrations, if these were striking enough to make a good show in a collection. This was still the almost universal practice when Holland's *Butterfly Book* was published (1898) and is strikingly evident in the many studies of infraspecific variation by Edwards. But long before, some collectors who had material from widely separated localities, noticed the fact of local variation and began to view locality records as something more than a mere convenient reminder of where to go for more of the species. Chief among these collectors was Staudinger of Dresden, who was comparing material from Mediterranean and northern Europe or blocks of material from central Asia with both; even in 1861 (the Staudinger and Wocke *Catalogue*) he was practically restricting the term "varietas" to such localisms. In his 1901 catalogue (Staudinger and Rebel), this was done as consistently as possible, and other types of variation were reduced to the designation "ab." Jordan, in England, adopted this definition, and it became rather general in Europe long before it was taken seriously over here, so that when the rather ambiguous terms of the International Code appeared, the official interpretation of the term "subspecies" soon became practically the "varietas" of Staudinger. Workers on the American fauna, even German workers on South American material, found the distinction impractical and never adopted it fully, though some tried to take advantage of the rules by calling the old traditional varieties "subspecies," especially where, as usually in mimetic South American types, there was a certain tendency to local restriction. This shows most strikingly in Stichel's revision of the heliconian butterflies in *Das Tierreich* (fasc. 22); but must be considered even in interpreting the lettered forms under the numbered species in McDunnough's *Check List*. The author has found a curious complication in *Junonia*, where racial limits appear to be somewhat different in the two biological phases of the buck-eye. As a result, before 1900 most of the infraspecific work was oriented to seasonal or genetic variation or to direct response to conditions, whereas most recent work has been on local variation, which can be more easily equated with the code concept of "subspecies." The most intensive studies have been a long series of papers by Roger Verity on European butterflies, largely aimed at tracing the presumable lines of migration of populations in past ages, and in America such studies as those of Gunder and of Hovanitz on local variation in California species of *Melitaea* and the species and near-species of *Colias* on both continents. Verity's great works are the *Rhopalocera Palaearctica: Papilionidae et Pieridae* (1905–1911); *Le Farfalle diurne d'Italia: Hesperides* in 1940; and his study of the Lycaenidae in 1943, with an amazing series of colored figures. But for the geography of the Nymphalidae we must still refer to his scattered papers. He belongs to the school which analyzes local variation on three levels: the race proper (which he calls *exerge*), the subrace (his race), and of course the unnamable field form.

SPHINGIDAE: The history of the Sphingidae for the century is short and simple, and for the most part distinct from that of any other group. When the century began, the authority for the United States was Harris' monograph (1839), cited above; then came Morris in 1862, and Boisduval's world revision in the *Suites à Buffon* (1874). In 1886 Grote and Fernald both published reviews based on Boisduval; Grote's was the one that covered North America, but my own early guide was Fernald's *Sphingidae of New England.*

The Rothschild and Jordan revision, published as a supplement to the *Novitates Zoologicae* in 1903, was a turning point, for it first put the classification on a solid basis, with keys as well as short descriptions for the whole world, and proper consideration of the genitalia. However, his names were applied according to an odd code of his own; when his use of an older name agreed with either tradition or later rules, it was pure coincidence. Early stages were also practically neglected and have never yet been studied from the world point of view. I studied the larval characters in 1911 (Ann. Entom. Soc. Amer., 4:261–280) under the encouragement of Beutenmüller, who had got together a good many specimens for a study of his own, then abandoned. Later I saw a few of them again in a most unexpected place. The only scientific approach to the pupae is by Mosher (*Ann. Entom. Soc. Amer.*, 11:403–442, 1918). The beautiful and detailed figures of Moss and of Bell and Scott ("Sphingidae of Peru," *Trans. Zool. Soc. London*, 20:65–118, 1912; *Nov. Zool.*, 27:333–424, 1920; *Fauna of British India*, "Moths," Vol. 5, 1937) give us a rich but superficial view of the exotic fauna.

Since, Beutenmüller's work on the adults has been mainly a modification of Rothschild and Jordan; but B. P. Clark's series of papers in the *Proceedings of the New England Zoological Club* have some important data on races in the United States, and have added a few, but very striking, species to our knowledge of other parts of the world. At the moment we have a fuller and sounder knowledge of the Sphingidae than of any other family of moths, yet scientifically the early stages are almost a blank, there being only those two hurried papers mentioned above, Miss Edna Mosher's on the pupae and mine on the larvae, each limited to a partial sample of the Holarctic fauna.

SATURNIOIDEA: Next to the sphinges, the saturnids are probably the most popular group of moths, but their discussion more properly belongs under biology rather than taxonomy, for knowledge of their early stages and biology has always anticipated their classification. In 1853 I suppose most people in the East knew them through Harris' *Insects Injurious to Vegetation;* and Boisduval supplied two California species from Lorquin's collecting. Clemens' revision in Morris' *Synopsis* then became the authority, and the four genera recognized by them (*Saturnia* and *Attacus, Ceratocampa* and *Dryocampa*) were the names familiar to amateurs until Holland's *Moth Book* came out in 1903. In fact, the saturnids were almost a specialty for amateurs and dealers, who knew how to find the cocoons, and who published some of the life histories in great detail. My own authorities "before Holland" were Harris' *Insects Injurious*, Mrs. Ballard's *Among the Moths and Butterflies* (1890), Mary Dickerson's *Moths and Butterflies* (1901) and Eliot and Soule's *Caterpillars and Their Moths* (1902). What Westerners did, I have no idea. But when Holland came out, we had colored figures of everything for the country, though we still used the four amateur authorities for biological data.

On the scientific side, the classification has never come properly into focus. Packard's revision for the National Academy was unfinished when he died. In its final publication it was rich on early stages, but fragmentary in classification. In Europe the picture was similar: plenty of material in the hands of dealers, including early stages, plenty of figures, and very little classification. Only this year have we at last a world classification (Michener, "The Saturniidae (Lepidoptera) of the Western Hemisphere," *Amer. Mus. Nat. Hist. Bull.*, Vol. 98, art. 5), which actually ties in most of the Eurasian types and leaves only the Africans incomplete. But still little has been done to work up the rich and significant larval and pupal characters. One might add that, in general, the family limits have been clearly understood for Europe and North America; South America, however, seems to have been a problem for many earlier authors, including Kirby in the *Catalogue of Lepidoptera Heterocera* (1892) who included most of the relatives of the Io moth in the Lasiocampidae, along with members of several other very distinct families.

BOMBYCES: That array of unrelated but similar families known colloquially as the bombyces have had too complex a history to follow in detail. In America the authority, as the century opened, was Morris; in Europe the second volume of Herrich-Schaeffer (1845) was available, and this was soon supplemented by Heinemann's *Schmetterlinge Deutschlands und der Schweiz* (1859), but during the whole period in Europe picture books have dominated the more serious classifications. In America the publication of

Neumoegen and Dyar's series of papers in the first two volumes of the *Journal of the New York Entomological Society* was an important event and so, in a less formal way, was Stretch's *Zygaenidae and Bombycidae*, published in parts. This last remained far from complete; the plates alone were finally published without color in the *Journal of the New York Entomological Society* in 1906. Hampson's *Catalogue of the Lepidoptera Phalaenae* (1898, 1900, 1901, 1914, 1920) gave us a world view for a few families (Euchromiidae, Nolidae, Arctiidae, Agaristidae, *s. str.*), but for the rest we still have only the colored figures and short descriptions in Seitz. In the first part of our century, and in earlier periods, this group was believed to be natural, being the *Phalaena Bombyx*, with a little of the *Sphinx*, of Linnaeus; but it was gradually realized to be heterogeneous, and the history of its major classification is that of the order as a whole.

NOCTUIDAE: The Noctuidae start our century in wonderful confusion, which has not yet been wholly cleared up; for Guenée and Walker published world revisions, while Herrich-Schaeffer, followed by Lederer, studied the European types more fully and presented keys. Each author divided the group into a series of families, but none defined them clearly, and no two wholly agreed. Also, it was already recognized that the deltoids belonged with the Noctuidae, rather than with the pyralids, but only Herrich-Schaeffer and Lederer made the union definite. There were also wide divergences in the use of generic names, which were reflected in this country by the divergent usages of Grote and Smith, followed later by Dyar and Hampson. Most works up to the First World War followed tradition more than rules, and diverged in their use of both; finally, after the war, more and more authors began using the code of 1911, but their individual interpretations added to the general confusion, and the rules often resulted in still further divergent uses of the older names. At the moment, from the world point of view, we have about three-quarters of the family in Hampson's *Catalogue of the Lepidoptera Phalaenae* and in Seitz, a complete view of the Palearctic fauna (such as it is) in Seitz, and the rest in fragments: the North American deltoids by Smith (1895); a catalogue including also the South Americans by Schaus (1916, with a key to genera); the fauna of British India (1895); and a host of loose descriptions. In the pseudodeltoids we actually have nothing since Walker—which means nothing at all, for very few were known then.

The subdivision of the family falls rather sharply into two periods. The early workers, like Guenée and Walker, divide it into a large number of weakly defined families; Lederer (1857) already saw it as a unit, but takes up these "families" in discussion; and through the rest of the nineteenth century we have general recognition of the family as single, but a similar protean series of groups, mostly treated as subfamilies. Hampson (1903) presented a new system of subfamilies, based chiefly on certain points used as key characters by Lederer; and these, though recognized as partly artificial, have been convenient enough to serve up to the present.

The Noctuidae even more than the skippers have been a main line in the study of genitalia. In 1857 Lederer was already examining all the available species and figuring the tips of valves. Smith, who for some decades was best known in this country for their study, also limited himself as a rule to the valves, usually pulling out and mounting a single valve, when he intended to save the specimen. About 1909 both Smith (with Grossbeck as technician) and Pierce in England began making more complete dissections on a large scale, and the younger group of workers have brought the technique to a very high level. (I was in the chain; Grossbeck taught me in 1910, and I showed some of the rudiments to Pearsall and Busck.)

GEOMETRIDAE: The geometers started the century just like the Noctuidae, with world reviews by Guenée and Walker and more precise analyses of characters by Herrich-Schaeffer and Lederer. Packard (following Guenée's system) gave us our bible for the family in 1876. The present system of subfamilies was established by Meyrick in 1892 (*Trans. Entom. Soc. London*), and adapted to our fauna by Hulst (*Trans. Amer. Entom. Soc.*, 23:245-386, 1896); and except for some primitive oddities can be considered fully natural, not a merely convenient grouping like the Hampson system in the Noctuidae. More recent work is scattered, and pretty tentative as regards tribes and genera; it takes the form of many small papers, and the fraction of a world revision written by Prout and published by Seitz. Work on genitalic characters is fragmentary and largely unpublished; that on early stages is mostly superficial, though study of the pupae is beginning to show some more significant characters.

PYRALIDIDAE: These again start with the same pattern: Guenée and Walker, Herrich-Schaeffer and Lederer, with Guenée introducing the system most used during the nineteenth century, and Lederer foreshadowing the system used most recently. But in these Pyralids Lederer did not finish his work, covering only the subfamilies grouping about the Pyralidinae and Pyraustinae and omitting the crambid and phycid-like types. This time the modern pattern of subfamilies and genera goes back chiefly to Hampson, in a series of catalogues (1895–1899), merely listing the species in most subfamilies, but describing and figuring the species of Phycitinae, Anerastiinae, and Galleriinae, with Ragonot, in volumes 7 and 8 of the Romanoff *Mémoires*. Beginning with this group Seitz fails us completely; and for species outside the last three subfamilies we have nothing beyond Guenée and Walker except the little group of revisions for North America following the break-up of the plan for a North American monograph: the Pterophoridae and Crambinae by Fernald, the Nymphulinae and Scoparias by Dyar, the few Macrothecinae by McDunnough.

MICROLEPIDOPTERA: The micros have followed a very different pattern, and a more complex one. American zoologists for the first fifty years usually treated the smaller species almost wholly from the point of view of biology, and there was a strong feeling that, in the larger genera like *Coleophora*, *Lithocolletis*, and *Nepticula*, adult characters hardly existed. Meanwhile a few stray workers were considering and describing the adults, but only three of these had any real influence: Brackenridge Clemens, especially after Stainton had reprinted his work as the *Tineina of North America* (1872), V. T. Chambers a little later, and Lord Walsingham, with his series of papers resulting from his trip to California and Oregon in the early 'eighties. When I started, the conventional way to "determine" a tineoid was to rear it, look up the food in Chambers' catalogue (*Bull. U. S. Geol. Surv.*, Vol. 4, no. 1, art. 4, 1878), check with Stainton's *Natural History of the Tineina* for the genus with similar behavior in Europe, and then come up with a guess at the species—the guess was occasionally correct. If it was a broad-winged species with less distinctive habits, we would cruise through Clemens.

In Europe the micros were arranged in orderly fashion somewhat earlier. In 1853 Herrich-Schaeffer completed the Lepidoptera, with keys and many figures, as a supplement to Hübner's Europeans. Somewhat later Heinemann reworked the fauna of central Europe (finished in 1877); and the picture books figured enough species to be serviceable. There was also the series of volumes of Stainton's *Natural History of the Tineina*, with their great contribution to the biology. Then, in the 'eighties and 'nineties Meyrick, in working out the Australasian fauna, developed an arbitrary but useful scheme of families for the micros, which he applied to the European fauna in his *Handbook* of 1895; and this was adapted to the American fauna by Busck in Dyar's *List*. Meanwhile Spuler had been working in Germany on a more natural system for the micros, partly in collaboration with Comstock's work on the macros; and the result appeared in Hormuzaki's *Analytische Uebersicht der palaearctischen Lepidopterenfamilien* (1904) and more fully though without any keys, in Spuler's own *Schmetterlinge Europas* (1910). We adapted it to the American fauna in the *Manual for the Study of Insects*, which then became again *An Introduction to Entomology*, and the first part of the *Lepidoptera of New York* (1920, 1924). The *Introduction* has in fact the later version, since the *Lepidoptera* was about four years in press. Scattered recent studies show the time is ripe for another reworking.

In the last half-century there have been a number of helpful revisions and catalogues, mostly of single families and altogether covering hardly half the micros. For central Europe we have Hering's contribution of the Lepidoptera to Brohmer's *Tierwelt Mitteleuropas;* and for the whole world we have Fletcher's catalogue of all the genera, with their references, types, type localities, and all their synonyms; also their families according to the Meyrick formula. The following list gives a summary of what we have. Note that the *Lepidopterorum Catalogus* (*Lep. Cat.*) is supposed to have a complete bibliography and general localities, but no descriptive matter; the scope of the *Genera Insectorum* (*Gen. Ins.*) is also world-wide, and gives descriptions and keys down to genus, but, as a rule, only original references. All but the Stenomidae are by Meyrick. The other works cited are for the Nearctic region only.

TORTRICIDAE (s. str.)	*Lep. Cat.*, 10, 1912; *Gen. Ins.*, 149, 1913.
OLETHREUTIDAE	Heinrich, U. S. Nat. Mus. *Bulls.* 123, 132, 1923, 1926.
PHALONIIDAE	Busck, *Journ. N. Y. Entom. Soc.*, 15:19, 1907 (omitting species of Phalonia).
CARPOSINIDAE	*Lep. Cat.*, 13, 1913; *Gen. Ins.*, 179, 1923.
YPONOMEUTIDAE (and *Plutellidae*)	*Lep. Cat.*, 19, 1914.
GLYPHIPTERYGIDAE	*Lep. Cat.*, 13, 1913; *Gen. Ins.*, 164, 1914.
HELIODINIDAE	*Lep. Cat.*, 13, 1913; *Gen. Ins.*, 165, 1914.
GELECHIIDAE	Busck, *Proc. U. S. Nat. Mus.*, 25, 770–930, 1903 (to species); Meyrick, *Gen. Ins.*, 184, 1925.
ŒCOPHORIDAE	Busck, *Proc. U. S. Nat. Mus.*, 35, 189, 1909 (to genus only); Meyrick, *Gen. Ins.*, 180, 1923.
BLASTOBASIDAE	Dietz, *Trans. Amer. Entom. Soc.*, 27, 100 ff; 1910.
STENOMIDAE	Busck, *Lep. Cat.*, 67, 1935.
COLEOPHORIDAE	(NE. U. S.) Heinrich, in *Lep. N. Y.*, 202–217, 1924.
GRACILARIIDAE	*Lep. Cat.*, 6, 1912; *Gen. Ins.*, 128, 1912; Ely, *Proc. Entom. Soc. Wash.*, 19:29–77, 1917 (U. S. genera and catalogue of species).
TINEIDAE	Dietz, *Trans. Amer. Entom. Soc.*, 31:1–96, 1905.
ADELIDAE (long-horns only)	*Lep. Cat.*, 6, 1912; *Gen. Ins.*, 133, 1912.
MICROPTERYGIDAE (and Eriocraniidae)	*Lep. Cat.*, 6, 1912; *Gen. Ins.*, 132, 1912.

Major Classification

The major classification and phylogeny of the order together have had rather a separate history. At the beginning of the century ideas of evolution had not become general, and most people were satisfied with approximations to the Linnaean system, supplemented by suggested cross-resemblances between the various groups, such as are represented in the diagrams in Herrich-Schaeffer by a web of lines and circles (e.g., vol. 6, pls. 1, 7, 15). Even in Herrich-Schaeffer's time it was realized that the "Bombyces" and "Tineina" were congeries of perhaps unrelated forms; yet the groupings are such a convenience that they are used even now to some extent.

After the Darwinian theory was digested, weblike classifications were recognized as artificial and there was a serious search for characters marking primitive or specialized forms, and indicating the lines of development. The most important early American work was by Packard, most fully published in the introduction to the *Monograph of the Bombycine Moths* (1895). In the same year Comstock published the *Manual for the Study of Insects*, with a key to the families defined on modern lines, and also a phylogenetic arrangement, notably breaking up the bombycine families and distributing them according to their true relationships. In the same period in Europe Spuler (from 1892) was working on adult, and Chapman (from 1893) largely on pupal, characters. Dyar came along immediately afterward with a more complete study of the larvae in a series of papers, starting with his "Classification of Lepidopterous Larvae" in 1894. The most productive point in Packard's study was the recognition of the very deep character of the differences between a few primitive families, in contrast to most of the order. Comstock became best known for his emphasis on the marked change of structure of the hind wing which set off the earlier "Jugatae" from higher types; but his distinction of "frenulum-losers" and "frenulum-conservers" has also turned out to be significant, when checked to the egg and larval characters discovered or emphasized by Dyar. It was only necessary to realize that the frenulum-losers included not only the families that had usually lost the frenulum, but also those, like the Geometridae, that showed merely a tendency to lose it (as worked out in Comstock's *An Introduction to Entomology* [1920] and my own *Lepidoptera of New York*).

Tutt, in his *British Lepidoptera,* presented a second system, especially in pages 102–128, of volume 1. His idea was that the Lepidoptera followed not one but two roughly parallel lines of evolution from the lowest to the highest branches. His wealth of argument and data gave him considerable authority for a time, but I think he no longer has any followers.

Later study of the auditory (or sonar) organs gave further emphasis to the "frenulum-conservers" as a unitary group. The organ itself has long been known, was first described in detail by Swinton in 1877, for a noctuid (*Entom. Monthly Mag.,* 14:123), and I got a glimpse of its phylogenetic value in 1916 (*Psyche,* 23:183), but it was not until Eggers' studies (1919, 1925, 1928) that its value was established. The organ is also useful below the family level, as has been shown by Richards (*Entom. Amer.,* vol. 13 (no. 1), 1933), working on the Noctuidae, and by Luh (thesis, published only in abstract) on the Arctiidae. At present Kiriakoff is working on other Noctuoidea.

Personally I stand by the system of the *Lepidoptera of New York* and the *Encyclopaedia Britannica* except for the micros, where recent work (notably that of Hinton) will probably result in some radical changes. But I fear no conventional classification will fully express the step-wise evolution of the forms lying below the Tineidae.

Some figures: The following counts will suggest the gradual increase in knowledge of the species of Lepidoptera. It is rather curious that the last complete catalogue of the order (Walker) lies in just the same period as the first for North America (Morris). All figures are rough, and the suggested totals for the world are merely guesses. The Harris catalogue (1833) was for Massachusetts only, and the total should be increased to allow for the Abbot discoveries published by Hübner and Smith; the Morris catalogue included Mexico and the West Indies.

WORLD FAUNA

	Noctuidae	*Micros*	*Total*
Linnaeus (1758)	66	104	535
Fabricius (1793–1794)	380	521	2,817
Hübner (about 1820)	784	709	4,198
Walker (about 1860, roughly)	5,625	8,800	33,600
Hampson (about 1910, partly estimate)	14,357	.....	.....
Present (pure guess)	18,500	25,000	80,000

NEARCTIC FAUNA

Harris, 1833 (Massachusetts only)	107	51	428
Morris, 1860 (North America)	486	236	1,551
Grote, Edwards, Chambers (about 1880)	1,409	1,482	4,544
Dyar (1903)	2,128	2,346	6,622
Barnes and McDunnough (1917)	2,532	3,439	8,495
McDunnough (1938–1939)	2,693	4,369	9,876

It appears that the Noctuidae (also the butterflies) are approaching complete discovery in the Nearctic, but that the other groups are due for substantial increase. The European list indicates that eventually there will probably be more micros than macros.

Morphology

The development of knowledge of the external morphology of the Lepidoptera has been almost wholly of two kinds, either incidental to general studies of the insects, like Crampton's work on a couple of types of Lepidoptera in 1908 and many later papers, or else by-products of classification studies. The study of internal anatomy, however, has been independent. For the caterpillar there has been nothing during the whole century in the class of Lyonet's work in 1760, and for the adult, the dissection of the Monarch, published by Scudder in the *Butterflies of Eastern North America* (pl. 62, 1888) stands alone. Further work on the anatomy has been voluminous but widely scattered; the fullest and most recent summary is that by Zerny and Beier in Kukenthal's *Handbuch* (vol. 3, pt. 2, 1936). It shows a fairly complete knowledge of the anatomy as a type, but there is still little on variation of structure within the order.

Physiology

Physiologists as a rule make slight distinction as to the form they use, whether *Neurospora* or *Paramecium, Drosophila* or man; only occasionally has a lepidopteran been chosen as an object, and I think never for the sake of contrast with other organisms. Quite recently Carroll Williams has been using caterpillars, chiefly the *cecropia* in the study of hormones and their relation to transformation or the mechanism of respiration and hibernation, with their controlling enzymes. Work on the nature of coloration has been more concentrated on the Lepidoptera, and it has been carried on for a longer period. Mason pretty well settled the problem of structural colors in 1927, followed by an actual electron photograph of the structures by Richards. But the question of pigments has been much more complex, though in recent years a number of workers, chiefly English, have done a good deal.

The matter of pattern, as distinct from color, should probably be considered morphology rather than physiology, since, though the elements generally appear in pigment, the pattern has the same fixity as morphological characters; it evolves from group to group in a similar way and is frequently foreshadowed by small but definite differences of structure in the individual scales. The realization that pattern elements have a fixity higher than the species or genus came pretty early. In America we are apt to associate it with Smith's diagram for the Agrotids (*Bull. U.S. Nat. Mus.*, vol. 38, 1890), but at the very beginning of our century Guenée had a labeled type pattern (*Species Général, Noctuélites,* pl. 1, 1851). The names of elements have been regularly applied to similar lines and spots in other families, but it has only been gradually apparent that many of these elements are homologous over a wide range of families. For the butterflies in particular an independent nomenclature has been developd, most fully worked out by Schwanwitsch (numerous papers, but the one on the *Catagramma* group [*Trans. Zool. Soc.,* 1939, pt. 2] is best known). It is for the future to show whether the nymphalid and noctuid schemes can be homologized definitely, but the absence of similarly definite schemes in the skippers, Castniidae, and Cossidae reduces our hope. The little work done on the physiological forces behind the forming of these patterns is too scattered to summarize.

The knowledge that coloration and patterns were protective by matching normal backgrounds, greatly antedates our time, but mimicry was a discovery of nearly one hundred years ago and was impressed on Bates (1862) by the wealth of examples he saw along the Amazon. A few years later, Müller was also impressed by the many cases he saw, farther south in Brazil, in which more than one member of a pattern appeared about equally protected, and proposed what we now call Müllerian mimicry (convergence of pattern to simplify the learning process, and thus to reduce the number of individuals sacrificed by inexperienced predators). Realization by North Americans that mimicry is also (though feebly) a North American matter dates from Scudder's *Essay* of 1889. Looking back we can date mimicry in a negative way to Linnaeus, for undoubtedly it was the handling of unrelated models and mimics with similar patterns that caused him to abandon, in his tenth edition, the very useful distinction of four-footed and six-footed butterflies.

For a full analysis of the problems involved in coloration, the critical work is certainly Gerald Thayer's *Concealing Coloration,* and the date is 1909. This work showed fully the functions of concealing pattern and color, mimicry, both tentative and developed, and added flash colors, ruptive pattern, and countershading—all largely illustrated by the Lepidoptera.[3] Later work has added many details, but little theory, much of which is summarized (without deep insight) in volume 2 of Schroeder's *Handbuch* (1929).

In the field of genetics the Lepidoptera have served from time to time, mainly at first in the breeding of families of specimens to obtain lots with aberrant patterns, and lots of material distributed by several dealers in the period after 1900 have been better known than the widely scattered publications. Seifert did some significant work in the early 1900's showing Mendelian inheritance, but his published reports in 1901 and 1905 do not deal with the genetics, which must be studied from his material preserved at the American Museum. Whiting worked on *Ephestia kuehniella,* and published some data on the genes in 1919, but soon abandoned the moth for its hymenopterous parasites. But the most important work based on the Lepidoptera was that on the gypsy moth, carried on by Goldschmidt over a period of many years, which threw light on the physiology of variation and the control of sex. It is summarized, with much other related material, in his *Physiological Genetics* (1938).

Geography

The Lepidoptera are a very important source of data for zoogeography, since in various groups we understand the classification well enough to distinguish between true relationship and parallelism; the material is widely collected, and the means of distribution are pretty well understood. Also, from the days of Wallace and Bates we have had workers interested in both Lepidoptera and

3. An interesting side note is the fact that Theodore Roosevelt used his term "nature-faker" chiefly of the Thayers—and it was they who turned out to be right.

geography, whose views were partly based on what they saw of the butterflies.

But much work has been invalidated by being based on false ideas of relationship. The most pretentious publication, Pagenstecher's *Geographische Verbreitung der Schmetterlinge* (1909) must be used with great caution, since at that time it was not yet possible in many cases to distinguish between relationship and parallelism, and current classifications were arbitrary systems for convenience in many instances in which he thought true relationship was intended. Schroeder's *Handbuch* (1929) also has a long chapter on zoogeography, based to a great extent on the Lepidoptera, but here again species lists are often presented without understanding. On a smaller scale we have studies of the spread of an immigrant in a new territory, such as Scudder's work on *Pieris rapae* (*Butterflies of Eastern North America,* p. 1175, *Mem. Boston Soc. Nat. Hist.,* 4:1), and the more recent governmental studies of the spread of the gypsy moth and the European corn borer (the last-named work very superficial). In Europe we have more detailed studies, based on the fuller data available, like Verity's papers on the significance of geographical variation, cited above, and Bryan Beirne's *Origin and History of the British Fauna* (1952).

Biology and Early Stages

Our story started with life histories: Aristotle's cabbage worm and silkworm, then Merian's one hundred fifty life histories from central Europe, and a somewhat smaller number from Surinam. For the European fauna a large number of naturalists made contributions to the Lepidoptera; but for the mere record of the appearance of the caterpillars, Hübner's *Geschichte* marks a high point, not touched before or since. After Hübner, the steady flow of contributions to life history continued, being integrated by Hofmann and again in Spuler's *Schmetterlinge Europas,* which shows plain signs of its background—Hübner, Hofmann, and post-Hofmann. For the more restricted fauna of the British Islands, manuals have come out every decade of the century, but the works of Stainton, Buckler, and Tutt must be mentioned.

In America the early work of Abbot in Georgia was mentioned earlier. Later, about 1900, there was great amateur activity in the northeast, best represented by the three popular works of that time, (Ballard, Eliot and Soule, Dickerson), already mentioned. For structure of early stages we have Fracker on the larva and Miss Mosher on the pupa, published by the University of Illinois in 1915 and 1916, respectively—studies which are a chief foundation of our modern classification—and also later papers by Miss Mosher on the Sphingidae, Saturnioidea, Notodontidae, and Geometridae. Finally, we have Peterson's *Larvae of Insects,* of which part 1 (1948) deals chiefly with the Lepidoptera.

In the foreign field data are still more scattered, but for some regions we have unified blocks of material: Matsumura's *6000 Insects* (1931) and the *Nippon Konshu Zukan* (1932), Lepidoptera by Esaki and others, for Japan; Burmeister's *Description Physique de la Republique Argentine* (1878) or the Lepidoptera parts of the *Fauna of British India* (1892–1947, and far from finished), especially the revised volumes on the Papilionidae, Pieridae, Nymphalidae, *s.l.,* except Nymphalinae, and Sphingidae.

For biology in the more restricted sense, the literature is so extremely scattered that we can only touch on the general works: Packard's *Guide for the Study of Insects* (1870), Berlese's *Gli Insetti* (1912–1920); Hering's *Biologie der Schmetterlinge* (1926), the second volume of Schroeder's *Handbuch* (finished in 1929), and Bourgogne's chapter on the Lepidoptera in the *Traité de Zoologie* (1951).

Economic Entomology

A review of the history of economic entomology is not a part of this report, but one may note that in this field also the Lepidoptera play a large part. The first serious report was probably Peck's article on the spring cankerworm (*Massachusetts Magazine,* 1795), which rated a frontispiece. Our century was marked by the inventions of high-pressure spraying apparatus to reach the gypsy caterpillars in the tall elms of eastern Massachusetts; and the caterpillars still hold their own as test objects, now that economic entomology has gone over from the study of insects to the study of spray chemicals.

Looking Ahead

This is a very difficult time to look ahead. One can try to extrapolate the present trends, making allowance for those that will last long and those that are ephemeral, or one may remember that our civilization is more than three quarters through the Petrie cycle, and that the next Dark Century is due in less than two hundred years.

The first prophecy is that there will be no lack of unknown material to work on. In a few groups, such as the fauna of west and central Europe, or the butterflies, bombyces, and noctuids of this country, there are few species to add, but in the micros here, and in all groups over most of the earth, even species-making is far from finished. I estimate that we know more than 90 per cent of the micros of Europe, well over half for the United States and Canada, but only a sample (mostly of those that can be easily caught and do not have to be reared) for the rest of the world.

For geographical study, the general laws of distribution are known, but they have been applied to the Lepidoptera only in a rudimentary way. It is high time for a new "Butterfly Geography" based on the better known groups, such as the butterflies, sphinxes, and saturnids, but usefulness of the other groups must wait for a sounder classification. That sounder classification in turn depends, in the higher forms, chiefly on the more complete study of known characters. The matter of major cleavages, the placing of aberrant types, and especially the evolution of the primitive families must wait in turn for morphology, and partly for internal morphology. Even in the better known higher types, vastly more study of the early stages is needed.

For morphology, especially internal morphology, one can find virgin territory anywhere in the order; while in comparative physiology and the scientific study of ethology one can say nothing yet has been done.

The brilliant, well-defined and well-understood pattern characters and the relatively easy breeding of the Lepidoptera make them fine objects for genetics, but so far relatively little has been accomplished. The sex mechanism, the reverse of that in the mammals or *Drosophila,* is a field for investigation. The nature of the species barrier is also a subject for study, through the various known and suspected "Rassenkreise," where one can say a population is a single species, or two, according to where in its distribution area it is studied. Goldschmidt has already studied the gypsy moth, in which the mechanism of sex determination is involved, but no one has touched *Utetheisa* (one species in the West Indies, two from Kansas to Texas) or the buckeye (one species in Mexico, two in Florida and Cuba). Biological rather than racial speciation is an open question in *Phyciodes tharos* and *P. batesi, Pieris oleracea* and *P. virginiensis, Halysidota tessellaris* and *H. harrisii,* in the oleaceous-feeding or *Triosteum*-feeding strains of *Adita chionanthi,* in the legume-feeding *Thanaos baptisiae* and *T. afranius* against the columbine-feeding *T. lucilius* and the salicaceous-feeding *T. persius,* and in many others.

Then there is enormous opportunity for biology in the truer sense, the study of living life: natural history, life histories of individual kinds, the interaction between any species and its environment, the seasons of species and strains, also behavior, and the like. This field has degenerated terribly in the last half of our century, largely, I believe, because so few people have the leisure to sit down and observe and so few live close enough to nature to be able to do so. Moreover, the study of the interaction between living creatures and their environment has become more and more sterile ever since it was christened "ecology." There are far more people who merely go through an area picking up and counting what they happen to find than there are people who know what even the commoner species are actually doing there.

So much for what the next half-century can find to do. When one tries to judge what it will actually be able to accomplish, one comes to the question of means. And this seems to depend on three main items: location, leisure, and money. There are certain things that money and only money can do, and the chief of these is publication. There is always room for notes, but public sale will not finance manuals, lists, compendia, and monographs in a field of few workers like entomology. These must be financed or research will cease for lack of record of discoveries. I got a bad shock a few months ago when the announcement of a large amount of money for research stated inconspicuously near the bottom that this money was not available for publication. If we are to have manuals, faunal lists, and integrated surveys of biological work, the money for publication must be earmarked before the work is started and must not be diverted. I know personally of three faunal lists that failed to appear after many hours of work, because the publication fund had vanished during the period of preparation. Also, five of the seven or eight missing volumes of Noctuidae of the *Catalogue of the Lepidoptera Phalaenae,* were actually prepared, but after the First World War there were no funds for printing. (I have been told that nomenclatural questions were also involved, but the part that was questioned for this reason was the only part actually published!) I therefore believe that the people who have control of research money, should use some of it for this type of work, and should guarantee the publication if the work is actually prepared in a period at all reasonable.

The other necessary factor is leisure, and this is a sociological problem, for which some of the foundations bear a heavy responsibility. For they have issued masses of propaganda against the amateur, and it is only the amateur who can have the requisite leisure. There is also the question of the university, for at the moment all our intelligent young people are encouraged, and almost forced, to go to the standardized universities. These are either located in cities or have so grown and destroyed their surroundings that their students are practically cut off from contact with living nature—not merely from the Lepidoptera. We need a drive against the academic degree as a thing of high value in itself, and a restoration of the types of education that give the young adult all the things that cannot be handled in the classroom (among them living biology, as well as the fine arts, business, geography, and the like). As far as our special field is concerned, a major offender is the so-called "Graduate Record Examination," which has been getting a good deal of prestige since the Second World War and which, so far as I can find out, gives practically no credit score for the things a good entomologist needs to have: independent thought, aptitude, knowledge of living biology as distinguished from textbooks, and the special skills that enable him to obtain and record his facts.

And I almost forgot the museums. They are necessary recording bodies, where all the tangible and durable sources of knowledge can be preserved. They can be sources of research in only part of the field, but from every biological problem enough material should go to a museum and be saved there to enable later workers to confirm that the person who did that piece of research had what he thought he had. The museum also needs money for housing and money for care; staff for routine work and also some staff members with leisure to follow up research leads as they appear.

This is the future for the Lepidoptera, as I see it, and equally for all fields of research in natural history. I leave it to the reader to decide how much is warning and how much prophecy.

COLEOPTERA

Melville H. Hatch
University of Washington, Seattle

These remarks on a century of progress in the study of beetles may be prefaced with the caution that neither the space at the author's disposal nor his knowledge permit more than the merest synopsis of the events involved. The men and books and institutions mentioned are examples only of complex movements, and important names frequently may have been left unmentioned.

In seeking, then, to survey the coleopterology of the last hundred years, we start with men studying beetles. Beetles occur wherever men do, but different beetles occur in different regions. The 3,711 species known from Great Britain (1945), the 8,473 species known from France (1935–1939), the 9,979 species and 4,409 varieties known from Italy (1929), and the 300,000 species known from the world are indices to the complexity of the problem.

Two approaches to coleopterology have developed. The study of local faunas has the advantage of being based on explorations that have been in month-by-month and year-by-year contact with the insects concerned. While decades of work may be required to bring the knowledge of a local fauna to reasonable completion, the problem is of limited scope and the data are close at hand.

On the contrary, the study of foreign faunas has the advantage of comprehensiveness and of greater opportunity for general conclusions. The drawback to the broader approach is the investigator's dependence on the work of incidental or itinerant collectors. One is at once removed from the data, and the world as a whole is so incompletely explored that conclusions tend to lose in permanence what they gain in comprehension. Both methods have operated together in the development of beetle studies and are, of course, strictly complementary. Those tremendous areas which lack resident collectors must be explored by the best methods available. The data obtained from the study of local faunas can be fully understood only when examined in the larger setting. It is profitable, however, to keep the two approaches in mind as we survey the history of the past hundred years of our science.

When, from the vantage point of some future century, the attempt is made to understand the development of the study of beetles, it will be seen that the hundred years just past have been part of a process of explosive development. From the perspective of a fully developed coleopterology—one that is, as a whole, at the same high level of development as the study of the German Coleoptera fauna now is the "Käferkunde" of the present with its 300,000 known species will seem as incomplete as now appear the 594 species of Linnaeus' *Systema Naturae* of 1758, the 22,399 species of Dejean's *Catalogue* of 1837, or the 77,000 species of Gemminger and von Harold's *Catalogus* of 1868–1876.

The modern study of beetles arose in northwestern Europe, in an area roughly bounded by Great Britain, France, northern Italy, Austria, Prussia, and southern Scandinavia, in the mid-eighteenth century. During its first hundred years it exhibited most of the tendencies which its second century has served to confirm and expand: the binomial nomenclature, the specific description, the descriptive monograph, the descriptive faunal catalogue and the faunal list, the world list, and the increasing facilities of entomological societies, journals, and musem collections. Even dichotomous analytical keys, which were first used for an entire beetle fauna in Redtenbacher's *Fauna Austriaca* (1849) were a product of this initial century. And in one respect this first century produced something that our second century has been unable to match, a descriptive catalogue of all previously described species, Fabricius' *Systema Eleutheratorum* (1801), containing 5,172 species. Shortly thereafter the number of known species became so great that no one has since brought them together in a single descriptive work.

As this first century advanced, the knowledge of beetles began to exhibit signs of maturity in portions of the area of its origin. This is shown particularly in Stephens' *Illustrations of British Entomology; Mandibulata,* Vols. I–V (1828–1832), in which 3,650 species of British beetles were distinguished, a number that was within 100 of the 1945 figure of 3,711. There has been, of course, much reshuffling of the names in this list in the intervening century. Stephens himself reduced the count to 3,470 in his 1839 *Manual,* and Crotch in 1866 could list only 3,081. But the point is that this was a working out of detail. To a first approximation, the British beetle fauna had been surveyed within seventy-five years of the tenth edition of the *Systema Naturae.*

At the same time that coleopterology was reaching maturity in its homeland, it was spreading east and west. Mannerheim (b. 1804, d. 1854) and Carl R. Sahlberg (b. 1779, d. 1860) represented the extension of beetle studies into Finland. In northeastern United States, Thomas Say (b. 1787, d. 1834) had described some 1,150 new species after 1818 and T. W. Harris (b. 1795, d. 1856) in 1833 had published a list of 994 species from Massachusetts.

The greatest coleopterist of this first century of the science was Count Auguste Dejean (b. 1780, d. 1845), peer and councilor of France. Dejean assembled the world's largest collection; he published extensively on the Carabidae of Europe and the world; and he issued a *Catalogue* of his collections, which in its last edition of 1837 enumerated 22,399 species and was as near to a world list as the period provided.

The Second Century of European Coleopterology

The opening of the second century of coleopterology found the French in the ascendancy and about to produce two of the sort of synthetic works which are perennially necessary in an expanding empirical science, if it is to be kept from falling into chaos. The *Genera des Coléoptères* of Th. Lacordaire (b. 1810, d. 1870) in twelve volumes (1854–1876)—the last three volumes by F. Chapuis (b. 1824, d. 1879)—provided a description of the genera of the world. The *Genera des Coléoptères d'Europe* by Camile Jacquelin du Val (b. 1828, d. 1862) and L. Fairmaire (b. 1820, d. 1906) in four large volumes (1854–1868), with 292 colored plates, gave keys to and descriptions of the European genera and a synonymical catalogue of the species.

At this same time W. F. Erichson (b. 1809, d. 1849), H. Schaum (b. 1819, d. 1865), G. Kraatz (b. 1831, d. 1909), and H. von Kiesenwetter (b. 1820, d. 1880) were working on the Coleoptera section of a *Naturgeschichte der Insecten Deutschlands* in many volumes. Volumes I to IV appeared from 1845 to 1867, covering Adephaga, Staphylinidae, Lamellicornia, and extensive portions of the Serricornia and Clavicornia.[1] Likewise incomplete and similarly ambitious was E. Mulsant (b. 1797, d. 1880) and Cl. Rey's (b. 1817, d. 1895) *Histoire Naturelle des Coléoptères de France* (1839–1884), still only fragmentary after the publication of thirty-seven volumes.

Not all the many-volumned faunistic surveys remained incomplete. C. G. Thomson's (b. 1824, d. 1899) *Skandinaviens Coleoptera* was finished in ten volumes, (1859–1868), and, somewhat later, W. W. Fowler's (b. 1849, d. 1923) *Coleoptera of the British Islands* appeared in five volumes (1887–1891), with 180 plates, illustrating about 2,230 species. Thomson, in particular, was a very able coleopterist. He split genera rather more finely than was acceptable in his day, but ever since his names have been coming slowly into general use.

The years 1862 and 1863 saw the publication of Hagen's *Bibliotheca Entomologica. Die Litteratur über das ganze Gebiet der Entomologie bis zum Jahre 1862.* A continuation of Hagen's *Bibliotheca* to cover the second century of Coleoptera studies is a desideratum that is only very partially met by the "Biblio-

1. The work was never completed, but later there appeared, in 1882, Vol. II(2), by E. Reitter (b. 1845, d. 1920) on Silphidae and allies; Vol. V (1877–1920), by G. von Seidlitz (b. 1840, d. 1917) on Anobiidae and extensive portions of the Heteromera; and Vol. VI (1881–1893), by J. Weise (b. 1844, d. 1925) on Chrysomelidae.

graphia Coleotterologica Italiana" in P. Luigioni's *Coleoterri d'Italia* (1929), the "Bibliography" in Leng's *Catalogue of the Coleoptera of America North of Mexico* (1920), with its five supplements (1927–1948); and Musgrave's *Bibliography of Australian Entomology* (1932).

In 1868 to 1876 there appeared in twelve volumes the *Catalogus Coleopterorum Hucusque Descriptorum* of M. Gemminger (b. 1820, d. 1887) and E. von Harold (b. 1830, d. 1886), enumerating about 77,000 species for the world.

In 1864 the Abbé S. A. de Marseul (b. 1812, d. 1890) established *L'Abeille,* the first journal devoted exclusively to the science of the Coleoptera. Twenty-six annual volumes of this periodical appeared to 1889. They contained monographic studies, occasional French translations of German papers, biobibliographical sketches of entomologists, and French translations of isolated descriptions of Old World beetles. After Marseul's death, publication became irregular and finally terminated with Vol. XXXVI (1938). Marseul's idea of a journal of coleopterology was imitated. Von Harold issued the *Coleopterologische Hefte,* Vols. I–XVI (1867–1879). M. Cheron issued fifteen numbers of *Le Coléoptèriste* (1890–1891); and Karl and Josef Daniel published ten numbers of their *Münchener Koleopterologische Zeitschrift,* Vols. I–III (1902–1908).

The two most important extant journals of beetle studies are the *Entomologische Blätter,* Vols. 1–48 (1904–1952), founded by H. Bickhardt, and the *Coleopterologische* (later *Koleopterologische*) *Rundschau,* Vols. 1–31 (1912–1948), founded by Adolf Hoffmann. Other more ephemeral serials were Pierre Lesne's *Coleoptera,* Vols. 1–3 (1925–1929); and Hans Wagner's *Coleopterologisches Centralblatt,* Vols. 1–6 (1926–1933). Adolf Horion's *Koleopterologische Zeitschrift,* Vol. 1 (1949) and G. Frey and Hans Kulzer's *Entomologische Arbeiten,* Vols. 1–3 (1950–1952) have started publication since the war. All these journals published important contributions and monographs in their day, but the bulk of coleopterological studies appeared in journals of general entomology or of even broader scope.

The second century of coleopterology had opened with coleopterists somewhat restive under the tarsomeral classification of Geoffroy (b. 1727, d. 1810). While this system indicated with some success such groups as the Heteromera or the Phytophaga-Rhynchophora complex or even the Coccinellidae, it utterly failed in the Staphylinidae, and Erichson was seeking for "natural" families. Darwin's *Origin of Species,* 1859, opened new vistas, but it was from the penetrating labors of Georg Seidlitz (b. 1840, d. 1917) of the University of Dorpat in Estonia that the modern classification really dated. Seidlitz' *Fauna Baltica. Die Käfer (Coleoptera) der Ostseeprovinzen Russlands* (1872–1874) not only provided a superior faunal work for a new area, but (pp. xxviii–xxx) gave an analysis of the order into ten major subdivisions which subsequent students have done little more than rearrange and rename. Outstanding among Seidlitz' successors was Ludwig Ganglbauer (b. 1856, d. 1912), Keeper at the Imperial Natural History Museum in Vienna. Ganglbauer, author of a superior but never completed descriptive catalogue of *Die Käfer von Mitteleuropa,* Vols. I–IV (1892–1904), proposed in 1903[2] the suborders Adephaga and Polyphaga, which have since dominated most thinking along this line.

---

2. Systematisch-koleopterologischen Studien, Münch. Kol. Zeit. I:271–319, 1903.

There is no opportunity here to review the numerous modifications that have been suggested in the Seidlitz-Ganglbauer classification. Abdomen, wing venation, male genitalia, female genitalia, head structure, larval structure have severally been explored for clues regarding the natural classification of the Coleoptera. The impression that one draws from such work is that the different special studies pretty much cancel each other out, and that the final word is still to be said.[3]

One of the most influential coleopterists at the middle of the second century of European coleopterology was Edmund Reitter (b. 1845, d. 1920). Beginning in 1878 Reitter wrote or edited, usually as a reprint series, the *Bestimmungs-Tabellen der Europäischen Coleopteren.* Some 123 numbers of this series, covering most of the families, had appeared by 1942. Eventually Reitter published one of our finest beetle faunas, the *Fauna Germanica,* Vols. I–V (1908–1916), with 168 colored plates illustrating about 2,775 species. With its 1935 *Nachtrag* by Adolf Horion, it is still the standard reference work on central European beetles. Another comprehensive faunal work for an important area is Porta's *Fauna Coleopterorum Italica,* 5 vols. (1923–1932), and its *Supplementum* I, (1934), and II (1949).

The classificatioin of beetle larvae is a difficult problem. Many species lead secretive lives, and their identity must usually be established in the first instance by rearing. As yet only the commoner species are known, even in Europe and America, but these are numerous enough so that diagnostic characters and keys have been worked out for the commoner genera and some of the species in most of the larger families, with the rather noteworthy exception of the Staphylinidae.

Studies of larval beetles, in the period under review, started with Chapuis and Candeze's *Catalogue des larves des Coléoptères* (Mém. Soc. Sci. Liége, VIII:341–653, 1855). In 1880, M. Rupertsberger (Biol. Käf. Eur., 295 pp.) listed 1,300 European species, the larvae of which were known, a figure that he increased to 1,700 in 1894 (Biol. Lit. Käf. Eur. von. 1880 an, 310 pp.). In 1891 W. Beutenmuller (Journ. New York Micr. Soc., VII:1–52) cited 372 North American species, the larvae of which had been noted; and in 1935 J. S. Wade (*A Contribution to a Bibliography of the Described Immature Stages of North American Coleoptera,* 114 pp.) listed 1,063 species. Among the more noteworthy works on larvae were: J. C. Schiødte's (b. 1815, d. 1884) *De Metamorphosi Eleutheratorum* (1861–1888), with its 88 beautiful copper plates; M. E. Perris' (b. 1808, d. 1872) *Larves de Coléoptères* (1877); A. G. Böving (b. 1869) and F. C. Craighead's (b. 1890) *Illustrated Synopsis of the Principal Larval Forms of the Order Coleoptera* (1931); and the section on Coleoptera in A. Peterson's (b. 1888) *Larvae of Insects.* Part II (1951). Recent keys to the families of larvae are found in Peterson's book and in F. I. Van Emden's "Larvae of British Beetles. III. Key to the Families" (Entom. Mo. Mag. LXXVIII:206–226, 253–272, 1942).

Meanwhile European coleopterists have been engaged in a continual assault on the foreign faunas. The museums in Paris, London, Berlin, Vienna, and else-

---

3. Noteworthy recent classifications are by Jeannel and Paulian, Rev. Fr. Ent. XI, 65–110, 1944; likewise expounded by these authors in Grasse's Traité de Zool. IX:892–1069, 1949; and that by R. A. Crowson being published currently in the Entomologists' Monthly Magazine.

where continued to expand their collections. One major instrument of advance was the world monograph. Marseul's *Histerides* (1853–1861), Candèze's *Elaterides* (1857–1900), Sharp's *Dytiscidae* (1882), Régimbart's *Gyrinidae* (1882–1907), A. Schmidt's *Aphodiinae* (1922), Jeannel's *Trechinae* (1926–1928), and Breuning's *Carabus* (1932–1937) are scattered examples of such studies.

A second approach was through the study of an entire exotic fauna. Wollaston's six volumes on the beetles of the Atlantic islands (1854–1867), and Sharp, Perkins, Blackburn, and others' six hundred pages on Coleoptera (1900–1910), in the *Fauna Hawaiiensis* illustrate this sort of work. The most elaborate study of a foreign fauna is Godman and Salvin's *Biologia Centrali-Americana.* The Coleoptera section of this lavish work appeared between 1880 and 1910 in 18 quarto volumes, 8,703 pages, listing 18,029 species (11,675 of them new), with 350 plates (297 colored), illustrating 8,596 species. No finer monument than this exists to the British at the apogee of their imperial and industrial power. The 17 volumes on beetles (1906–1939) in the *Fauna of British India,* represent a partial study of another enormous beetle fauna.

A third approach to the problem of the world fauna is through the study of a restricted group for a restricted area. Among the more impressive recent examples may be cited A. Hustache's *Curculionides de Madagascar* (1924, 582 pp.), R. Jeannel's *Coléoptères carabiques de la région malgache* (Madagascar 1946–1948, 1146 pp.), and P. Basilewsky's *Harpalinae de'Afrique et de Madagascar* (1950–1951, 616 pp.).

P. Wytsman's *Genera Insectorum* (1902–1938) was an attempt—never completed—to describe the genera of the world and list the species. Most of the 75 fascicules devoted to beetles were small, but the following were among the more sizable: Buprestidae by C. Kerremans (1902–1903); Elateridae by O. Schwarz (1906–1907), Pselaphidae by A. Raffray (1908), Cicindelinae by W. Horn (1908–1915), Histeridae by H. Bickhardt (1916–1917), Aleocharinae by A. Fenyes (1918–1921), Carabinae by M. G. V. de Lapouge (1929–1932), Lagriidae by F. Borchmann (1936). The Junk-Schenkling *Coleopterorum Catalogue* (1910–1940, 31 vols., nearly 25,000 pp.) provided a bibliographical catalogue of about 215,000 species. *Supplementa,* under the editoriship of W. D. Hincks, began appearing in 1950. Winkler's *Catalogus Celeopterorum Regionis Palaearcticae* (1924–1932) involved the expansion of the conventional European catalogue to cover a wider area.

What may be said of the new points of view that have appeared in this century in European coleopterology in addition to the continued spectacular development indicated in the foregoing paragraphs?

First, there is the greater detail of the more recent work. Darwin showed that only individuals exist, and taxonomists followed by insisting on basing their studies on ever-increasing series of specimens. Moreover, with the growth of distributional and ecological studies, there is an increasing insistance on the attachment to the individual specimens of precise data on locality, date, habitat, and collector.

Second, there was the widespread tendency on the Continent to investigate infraspecific variation, with the result that large numbers of geographical varieties or subspecies and nongeographical varieties or aberrations have been described and named. The description and naming of very numerous nongeographical variations has occurred especially in species with variable color patterns belonging to such genera as *Cicindela* and *Nicrophorus* and to families like Coccinellidae, Cerambycidae, and Chrysomelidae. The result was that Luigioni's catalogue of *I Coleotteri d'Italia* (1929) listed 9,979 species, 1,371 subspecies, and about 3,100 aberrations in that fauna.

Third, there was the discovery of the great utility of the male genitalia in the separation of species. In many genera species that can be separated only with great difficulty or not at all on the basis of external structure are readily distinguished by aedeagal characters. The result has been a growing tendency in the last thirty or forty years to employ genital characters in distinguishing species, and some authors go to the extreme of regarding their figures of the genitalia as sufficient exposition of the differences involved without supplementary verbalization.

The present interest in beetles in Europe seems unabated at both the professional and amateur levels. Virtually every country from the British Isles and France to Rumania and Russia has the requisite faunal works to aid and encourage such studies. Paulian (Col. Bull. II:42, 1948) tells of an amateur group, the "Coléoptèristes de la Seine," with more than two hundred members in Paris alone. France, Sweden, and the USSR have elaborate works on their faunas in process of current publication. In Germany there is the incredible detail of O. Rapp's *Käfer Thüringens* (1934–1935, 3 vols., 2,000 pages). This work starts with a list of 389 men who have contributed to the coleopterology of Thuringia. This is followed by bibliographic, distributional, and ecological data on 4,381 species, and the book concludes with an exhaustive reanalysis of the list in terms of habits and habitats. Adolf Horion, moreover, is currently issuing a new *Verzeichnis der Käfer Mitteleuropas* (Abt. 1, 1951) and an extremely detailed critical *Faunistik der Mitteleuropäschen Käfer* (Bd. I, 1941; Bd. II, 1949).

The one somber note is struck by the Communist government of the USSR. Since the 'twenties the Russians have been unwilling to allow non-Communist foreigners to collect insects in their domain, and since World War II, this same prohibition has been extended to large areas in both Europe and Asia. In retaliation, moreover, extensive areas of the West are closed to the Communists. The result is that it is impossible at present to assemble by direct field work a world collection. It is to be hoped that such conditions will not long endure.

In another respect, likewise, the Russian Communists are exerting an unfortunate influence on the study of beetles. Beginning in 1936 the Academy of Sciences of the USSR began to issue a Coleoptera section of the *Faune de l'URSS* on a scale that promised to make it one of the great Coleoptera faunas, subjecting the beetles of the vast Russian empire to precise analysis. The first volumes were mainly in Russian, but contained extensive appendices giving German translations of the keys and of the descriptions of the new species, thus making the analysis available to an international audience. Parts issued in 1950 change this arrangement. The French title page and all sections in German, including descriptions of new species, have been eliminated, thus violating the specific recommendation of the International Code of Zoological Nomenclature. This vastly limits the international utility of the books and suggests that new names so proposed may be regarded as *nomena nuda*.

American Coleopterology in the Last Hundred Years

American coleopterology first developed in the area between Washington and Boston. Say's contacts were with Dejean in Paris, and, later, LeConte and Horn were in touch with colleagues in both France and Germany. The history of the study of beetles in America was conditioned primarily by the vast hinterland which lay just beyond the Appalachian Mountains and which by 1850 extended without political or linguistic barrier all the way to the Pacific Ocean.

If the situation had been different—if the Americans had been firmly hemmed in to their north Atlantic homeland or if they had been broken into several linguistic groups—American coleopterology might well have developed in accordance with the European pattern of increasingly detailed studies of restricted regions. Harris' 1833 list of the beetles of Massachusetts might well have developed into a Massachusetts or a New England fauna.

But the spell of a continent proved too strong. On the one hand, it gave a practical turn to the American mind which allowed but slight attention to such an esoteric pursuit as the study of beetles. On the other hand, it meant that such coleopterists as did appear were completely absorbed in analyzing the fauna of an entire continent. They had no energies either for the detailed local studies so conspicuous on the European scene or for the world studies which likewise, from the beginning, attracted the attention of the Europeans. The literature which did emerge took the form, almost exclusively, of technical monographs, continental in scope, with the result that not many persons were attracted to the study and that American coleopterology has remained the pursuit of a few professional entomologists.

The father of American coleopterology was John Lawrence LeConte, M.D. (b. 1825, d. 1883), of New York and Philadelphia. A man of independent means, LeConte between 1844 and 1884 described 4,816 species of beetles in nearly all families, of which 864 were considered synonyms in 1881. Moreover, as a rule, LeConte's species were not announced in isolated publication but in monographs which treated the whole continent. LeConte accompanied Louis Agassiz to Lake Superior in 1849. In 1850 and 1851 he was collecting in California and the Southwest, and in 1869 to 1872 he visited Europe, studying Kirby and Walker types in the British Museum and visiting Continental coleopterists.

In 1853 LeConte joined with F. E. Melsheimer (b. 1782, d. 1873) and S. S. Haldeman (b. 1812, d. 1880) of Pennsylvania in producing a *Catalogue of the Described Coleoptera of the United States,* listing 4,750 species. In 1859 he edited a collected edition of *The Complete Writings of Thomas Say on the Entomology of North America,* with accompanying commentary. Since Say's collections had not been preserved, it was necessary to come to some understanding of his species as a basis for further studies. In 1861–1862 LeConte published Part I of a *Classification of the Coleoptera of North America,* giving the generic classification of the families except Coccinellidae, Phytophaga, and Rhynchophora. Part II, on Cerambycidae, appeared in 1873, but the completed work, by then revised, did not appear until a few months before LeConte's death in 1883, and then in collaboration with George H. Horn.

LeConte's collection went to Agassiz' Museum of Comparative Zoology at Harvard. Of the 9,100 or 9,200 species of North American beetles known at the time of his death, LeConte had described over two-fifths. In his day he was particularly noted for his distributional studies and his suggestion that the Rhynchophora constitute one of the two primary subdivisions of the Coleoptera. In our greater perspective, it is realized that his real claim to fame is the broad descriptive basis that he laid for the study in North America of the entire order.

Among the younger contemporaries and successors of LeConte who produced important monographic studies were George H. Horn (b. 1840, d. 1897), who described 1,582 new species, Frederick Blanchard (b. 1843, d. 1912), William G. Dietz (b. 1848, d. 1932), John B. Smith (b. 1858, d. 1912), Charles W. Leng (b. 1859, d. 1941), Roland Hayward (d. 1906) H. C. Fall (b. 1862, d. 1939), who described 1,453 new species, Charles F. A. Schaeffer (b. 1860, d. 1934), and E. C. Van Dyke (b. 1869, d. 1952).

Meanwhile the indigenous study of beetles was spreading. By 1869 Johnson Pettit (d. 1898) was publishing on beetles in Ontario and Abbé Leon Provancher (b. 1820, d. 1892) in Quebec. H. G. Hubbard (b. 1850, d. 1899) and E. A. Schwarz (b. 1844, d. 1928) were at work in Detroit in the middle 'seventies, and by the late 'seventies Charles Dury (b. 1847, d. 1931) at Cincinnati and F. H. Snow (b. 1840, d. 1908) at Lawrence, Kansas, had taken up their investigations. The 'eighties saw John Hamilton (b. 1827, d. 1895) busy at Pittsburgh, G. W. Taylor (b. 1851, d. 1912) at Victoria, B. C., and H. F. Wickham (b. 1866, d. 1933) at Iowa City; and by the 'nineties H. C. Fall and Frank E. Blaisdell (b. 1862, d. 1947) were at work in California.

Turning to synthetic works, catalogues or supplements to catalogues of Nearctic species have been produced in 1863–1866, 1873, 1880, 1885, 1887, 1889, 1895, 1920, 1927, 1933, 1939, and 1948. Provancher in 1877 published a *Petite Faune Entomologique du Canada,* Vol. I. "Les Coléoptères," describing about 950 species from Quebec and Ontario. Hamilton's *Catalogue of the Coleoptera Common to North America, Northern Asia, and Europe* (Trans. Amer. Entom. Soc., XVI:88–162, 1889; ed. 2, *ibid.,* XXI:345–416, 1894) and *Catalogue of the Coleoptera of Alaska (ibid.,* XXI:1–38, 1894) were important synthesizing works. Wickham in his "Coleoptera of Canada" (1894–1899), published in parts in the *Canadian Entomologist,* gave keys to the species of a number of families for Ontario and Quebec.

In 1910 appeared *The Coleoptera of Indiana* by W. S. Blatchley (b. 1859, d. 1940), which, in conjunction with Blatchley and Leng's *Rhynchophora of North Eastern America* (1916), provided a descriptive catalogue of 2,954 species of beetles from Indiana. Written in the tradition of LeConte and Horn, with its division into Genuina and Rhynchophora, this is the only complete descriptive beetle fauna, except Provancher's provisional work, produced so far in North America.

Leng's catalogue of the *Coleoptera of America North of Mexico* (1921), broke with the LeContian tradition and integrated American studies with those that had been going on in Europe. M. H. Hatch's (b. 1898) *Indices* to keys and local lists (1927–1928) (Journ. New York Entom. Soc., XXXV:279–306, 1927; XXXVI:335–354, 1928; XXXVII:135–143, 1929; XLIX:21–42, 1941) organized aspects of the literature, and J. C. Bradley's (b. 1883) *Genera of Beetles of America North of Mexico* (1930) provided a much-needed revision of LeConte and Horn's *Classification.*

Between 1884 and 1924 Thomas L. Casey (b. 1857, d. 1925) described some 9,400 species, mostly from the Nearctic region. Large numbers of these were based on evanescent differences and are invalid by conventional criteria. W. Horn (1915) rejected 86 out of 99 of Casey's names in Cicindelidae; Leng (1920) rejected 144 out of 150 names in Buprestidae and 30 out of 34 names in Prionini; Bänninger (1950) could recognize only one out of 24 names in Pasimachus; and Karl Holdhaus (Schröder's *Handb. d. Entom.* II:899, 1927) complained that Casey had so multiplied species in numerous families as largely to conceal the true status of the Nearctic fauna. Casey left his collection to the National Museum, and, whatever one thinks of Casey's work, there can be nothing but praise for the generous, intelligent cooperation shown by Mrs. Casey and the officials of the Museum in preserving his material for future students.

The almost exclusive preoccupation of Americans with their own fauna has already been noted. G. H. Horn covered Throscidae and Eucnemidae in 1890 for the *Biologia Centrali-Americana;* A. Fenyes (b. 1863, d. 1937), of Pasadena, covered Aleocharinae for *Genera Insectorum* (1918–1921); and M. H. Hatch, of Seattle, did the Silphidae (1928) and Leiodidae and Clambidae (1929) for the *Coleopterorum Catalogus.* But such contributions only served to emphasize the general absence of Americans from the international scene.

American interest in the Neotropical fauna was signalized in 1914 when Leng, in collaboration with A. J. Mutchler (b. 1869), of the American Museum, published a *List of the Coleoptera of the West Indies (Bull. Amer. Mus. Nat. Hist.,* 33:391–493). W. S. Fisher (b. 1878), at the United States National Museum, revised the West Indian Buprestidae in 1925 (Proc. U. S. Nat. Mus., 65(9):1–207) and he and other coleopterists at that institution displayed a persistent interest in the Neotropical fauna, which culminated in R. E. Blackwelder's (b. 1909) *Monograph of the West Indian Staphylinidae* (*Bull. U. S. Nat. Mus.,* No. 182, 1943) and *Checklist* of Neotropical Coleoptera, 1944–1947 (*Bull. U. S. Nat. Mus.,* No. 185). The opening up of automobile communication with Mexico in the 'thirties and other factors stimulated contacts with the south, which have resulted in contributions to the knowledge of the Neotropical fauna by Orlando Park (b. 1901), of Northwestern University, in Pselaphidae, E. G. Linsley (b. 1910), of the University of California, in Cerambycidae, M. A. Cazier (b. 1911), of the American Museum, and numerous others. World War II similarly served to broaden American horizons so that, for instance, P. J. Darlington (b. 1904), of Harvard, is devoting himself to circumtropical Carabidae.

The limited status of coleopterology in the United States is revealed by the fact that a year after its founding in 1949 a Coleopterists' Society had only 186 members, and died in 1952. The largest group of coleopterists in the country is at the National Museum in Washington, where E. A. Chapin (b. 1894) is curator and where the economic importance of the order assures the continuation of a staff interested in beetles. Similar economic motives also assure the permanence of such studies at Ottawa, where W. J. Brown (b. 1902) has been in charge of Coleoptera since 1927. Sizable groups of coleopterists are likewise centered at the Chicago Museum, where R. L. Wenzel (b. 1915) is curator, and in the San Francisco Bay area, where E. S. Ross (b. 1915) is curator at the California Academy of Sciences and E. G. Linsley chairman of the Department of Entomology at the University of California. This last institution, in particular, since well before E. C. Van Dyke's retirement in 1939, has trained a notable series of able coleopterists.

In 1947 R. H. Arnett (b. 1919), then at Cornell University, founded *The Coleopterists' Bulletin,* the first American journal of coleopterology.

Coleopterology in Australia, New Zealand, and Elsewhere

Indigenous coleopterology in Australia dates from the founding of an Entomological Society of New South Wales in Sydney in 1862 by Sir William Macleay (b. 1820, d. 1891), the Reverend R. L. King (b. 1823, d. 1897), and others. George Masters (b. 1837, d. 1912) published a *Catalogue of the Described Coleoptera of Australia* in 1871, with a second edition in 1885–1887 and a supplement in 1895–1896. The Reverend Thomas Blackburn (b. 1844, d. 1912) described 3,069 species of Australian beetles between 1888 and 1912. Other noteworthy students of Australian Coleoptera have been T. G. Sloane (b. 1858, d. 1932), a specialist on Carabidae; A. M. Lea (b. 1868, d. 1932), of the South Australian Museum at Adelaide, and H. J. Carter (b. 1858, d. 1940), who deposited his collection in the National Museum at Melbourne. A. Musgrave (b. 1895) published a useful *Bibliography of Australian Entomology* in 1930. In 1926 there were 16,660 species of Coleoptera known from Australia.

The indigenous study of New Zealand Coleoptera is virtually the work of one man, Major Thomas Broun (b. 1838, d. 1919), of Auckland. During thirty-nine years preceding his death Broun described some 4,323 species from the archipelago, of which about 3,500 were named by him. G. V. Hudson in his interesting book, *New Zealand Beetles* (1934), suggested that perhaps as many as half of Major Broun's species may be synonyms!

The author of this paper lacks the knowledge, even if he were permitted the space, to attempt a country-by-country evaluation of Coleoptera studies. Southern South America is the site of some work, of which Carlos Bruch's (b. 1869, d. 1943) *Catálogo Sistemático de los Coleópteros de la República Argentina* (1911–1914), with *Suplemento* I–IV (1915–1928), is an outstanding example. South Africa is likewise the home of some indigenous study of beetles, the Belgian-born L. A. Peringuey (d. 1924) having been one of the leading contributors.

Indigenous coleopterology developed late in Japan, where most of the species have been described by Europeans. H. Kono, T. Kano, and Y. Miwa are outstanding among Japanese coleopterists, the last being the author of *A Systematic Catalogue of Formosan Coleoptera* (1931). In China, before the Communist revolution, a certain amount of coleopterological work was under way, especially at some of the Japanese- and American-sponsored institutions. Y. Ouchi's *Biographical Introduction to the Study of Chinese Insects* (1934), C. F. Wu's *Catalogus Insectorum Sinensium,* Vol. 3, "Coleoptera" (1937), and J. L. Gressitt's *Longicornes de Chine* (1951) are examples. In Hawaii, E. C. Zimmerman (b. 1912) has been studying the beetles of Oceania since 1934.

Fossil Beetles

The early students of fossil beetles, like O. Heer (b. 1809, d. 1883) and S. H. Scudder (b. 1837, d. 1911), assigned the remains with great exactness to living genera. By 1908 some 352 species of Mesozoic and 2,559 species of Cenozoic beetles had been described, nearly all from Europe and North America. Beetle fossils, however, consist almost exclusively of impressions of elytra and pronota. In view of the slight extent to which characters drawn from these parts are decisive in the classification, A. Handlirsch (b. 1865, d. 1935) in his *Fossilen Insekten* (1908) suggested that, so far as the Mesozoic remains were concerned, the record revealed no more than the presence of certain general coleopterous types, such as carabid, elaterid, buprestid, and hydrophilid. The Tertiary remains, however, even as far back as the Eocene, continue to be placed in such living genera as *Lebia, Harpalus, Bembidion, Platynus, Berosus, Tropisternus, Bledius, Lathrobium, Cryptocephalus,* and *Sitona.*

So far as the elucidation of interglacial and postglacial remains of beetles is concerned, a good deal of progress is being made by a more intensive study of the characteristics of the elytra and pronotum of living species. Much further back in the geological record than this, however, the writer feels that coleopterists probably must be satisfied with form-genera, many of which may never be integrated satisfactorily in the classification of living types.

In 1924, Tillyard (Proc. Linn. Soc., New South Wales, 49:429–435, 1924) described six species of Coleoptera from the Upper Permian of New South Wales along with a beetlelike wing cover exhibiting true venation, which he ascribed to a new order, Protocoleoptera, close to the ancestry of the Coleoptera. A. V. Martynov (b. 1870, d. 1938) in 1933 reported beetles from the Permian of Russia, and Jeannel (1947) erected a suborder Archicoleoptera for these Permian beetles. Jeannel, furthermore, has shown considerable enthusiasm for the Gondwanaland hypothesis and Wegener's "wandering continents" as an aid in understanding beetle distribution, but there are many who disagree with him.

Prognostication of the future of coleopterology is uncertain. If it follows the pattern of a relatively mature science like ornithology, the time will come when beetles everywhere, in both adult and larval stages, will be as well known as are now the adult stages of central and northwestern Europe. The geographical variability and the ecological relationships of the species, likewise, will be worked out. Many years will be required to realize such a program!

STREPSIPTERA

R. M. Bohart
University of California, Davis

The status of knowledge in the order Strepsiptera in 1853 is indicated by the fact that only 5 of the 23 currently known genera had been described and these represented only 3 of the 5 families as we now know them. Some two dozen authors had contributed descriptions and figures dealing with a total of 11 species but had devoted most of their publications to a discussion of the phylogenetic relationships of these peculiar insects. The first strepsipteran was described by Peter Rossi in 1793 and twenty years later, in 1813, Kirby erected the order Strepsiptera. This did not find favor with the majority of taxonomists, and the group was placed generally in the Coleoptera or less frequently in the Diptera, Neuroptera, or Hymenoptera.

In the following fifty-five years only 3 more genera were described but our knowledge was increased to a greater extent along other lines. The only fossil strepsipteran now known, *Mengea tertiaria* Grote, was reported by Menge in 1866 in Baltic amber. This indicated that the order had not changed greatly since Tertiary times. In 1893 Nassonow gave the first account of internal anatomy and his work is still the best available on the subject. Another step forward was a paper by Perkins in 1905, which described the life histories of several parasites of leafhoppers and suggested their possible importance in biological control.

The stage was set for an expansion of the Strepsiptera along systematic lines, and from 1909 to 1918 W. D. Pierce dominated this field. Holding stubbornly to a theory of host-parasite specificity, Pierce raised the number of described species by 1918 to a total of 166, which he distributed among 5 superfamilies, 11 families, 8 subfamilies, 5 tribes, and 49 genera. Fortunately, later workers have been able to reduce this top-heavy structure to 6 families and 16 genera, to which 7 more have been added. The chief value of Pierce's papers was that they assembled for the first time all the scattered references to the order so that workers in various parts of the world could proceed on a common basis.

At this time (1918) it was thought that all female Strepsiptera were endoparasitic for life, beginning with the second larval stage. This idea was blasted by Peyerimhoff, who described the free-living female of *Eoxenos* in 1919. Another major contribution was that of Salt (1927) dealing extensively with the effects of stylopization. He pointed out that in the Hymenoptera those hosts which had a fixed amount of larval food, such as the solitary Vespidae, frequently assumed the characters of intersexes, whereas the hosts continually fed as larvae, such as the social Vespidae, exhibited no such external differences. The work of Peyerimhoff bore fruit after fifteen years when, in 1934, Parker and Smith associated the female *Eoxenos* with a mengeid male and established the female of the Mengeidae for the first time. All that remained to complete the skeleton framework of the picture in this family was to find the host. This turned out to be a thysanuran, as reported by Carpentier in 1939. In the same year Ogloblin published the first evidence of females in the family Myrmecolacidae. His startling finds indicate that the males parasitize ants and the females mature in various types of Orthoptera. Also in 1939, Lindberg, working with *Elenchus* parasitic on a fulgorid, gave the first complete record of the relationship between a strepsipteran and its host.

The first major review of the order since that of Pierce in 1918 was attempted by Bohart (1941) who revised the world genera and the species of North America. It was here that many of the superfluous categories of Pierce were synonymized. Bohart followed this with the first comprehensive paper on the leafhopper parasite family Halictophagidae in 1943. Also in 1943, Hofeneder and Fulmek published a complete cross-reference catalogue to the parasites and their hosts, and Silvestri gave a comprehensive treatment of the biologies of 6 Italian species of *Mengenilla*.

At present there are only a few workers actively publishing papers on the Strepsiptera. Certainly one reason for this is the difficulty of getting enough material for study. Male specimens, which offer the best characters for systematic study, are generally rare. Exceptions to this rule have been pointed out by MacSwain (1949), who collected 510 male *Stylops* by exposing 8 caged females, and by Bohart (1951), who reported nearly 300 male myrmecolacids taken at light in the Philippines by E. S. Ross and by H. Hoogstraal.

Although the idea of complete host-parasite specificity has been largely discredited, the controversy with respect to the phylogenetic position of the order still continues. Probably the majority of systematists favor the ordinal status but a strong minority would place these insects with the Coleoptera, and a dissident few attempt to relate them to whiteflies and scales.

REFERENCES

Bohart, R. M.

1941. A revision of the Strepsiptera with special reference to the species of North America. Univ. Calif. Publ. Entom., 7:91–160.

1943. New species of *Halictophagus* with a key to the genus in North America. Ann. Entom. Soc. Amer., 36:341–359.

1951. The Myrmecolacidae of the Philippines. Wasmann. Journ. Biol., 9:83–103.

Carpentier, F.

1939. Sur le parasitisme de la deuxième forme larvaire d'*Eoxenos laboulbenei* Peyer. Bull. and Ann. Soc. Entom. Belg., 79:451–468.

Hofeneder, K., and L. Fulmek

1942–1943. Verzeichnis der Strepsiptera und ihrer Wirte. Arb. physiol. agnew. Entom. Berlin-Dahlem, 9:179–185, 249–283; 10:32–58, 139–169, 196–230.

Kirby, W.

1813. Strepsiptera, a new order of insects. . . . Trans. Linn. Soc. London, 11:86–123.

Lindberg, H.

1939. Der Parasitismus der auf Chloriona-Arten lebenden Strepsiptere *Elenchinus chlorionae* n. sp. sowie die Einwirkung derselben auf ihren Wirt. Acta Zool. Fennica, 22:1–179.

MacSwain, J. W.

1949. A method for collecting male *Stylops*. Pan-Pac. Entom., 25:89–90.

Menge, A.

1866. Ueber ein Rhipidopteren und einige andere im Bernstein eingeschlossene Tiere. Schr. Naturf. Ges. Danzig, ser. 2, 1:3–4.

Nassonow, N. V.

1893. On the morphology of *Stylops melittae*. Warsaw Univ. News (1893), pp. 1–30. (In Russian.)

Ogloblin, A. A.

1939. The Strepsiptera parasites of ants. 8th Internat. Congr. Entom. Berlin, Verhandl., 2:1277–1284.

Parker, H. L., and H. D. Smith

1934. Further notes on *Eoxenos laboulbenei* Peyerimhoff, with a description of the male. Ann. Entom. Soc. Amer., 27:468–479.

PERKINS, R. C. L.

1905. Leafhoppers and their natural enemies. Hawaiian Sugar Planters' Assn. Exper. Sta. Bull., 1:90–111.

PEYERIMHOFF, P.

1919. Un nouveau type d'insectes Strepsiptères. Bull. Soc. Entom. France, 1919: 162–173.

PIERCE, W. D.

1909. A monographic revision of the twisted-winged insects comprising the order Strepsiptera Kirby. Bull. U. S. Nat. Mus., 66:1–232.

1918. The comparative morphology of the order Strepsiptera together with records and descriptions of insects. Proc. U. S. Nat. Mus., 54:391–501.

ROSSI, P.

1793. Observation de M. Rossi sur un nouveau genre d'insecte, voisin des Ichneumons. Bull. Soc. Philom. Paris, 1:49.

SALT, G.

1927. The effects of stylopization on aculeate Hymenoptera. Journ. Exper. Zool., 48:223–331.

SILVESTRI, F.

1943. Studi sugli "Strepsiptera" III. Descrizione e biologia di 6 specie italiane di *Megenilla*. Boll. Lab. Zool. gen. agrar. Fac. Agrar. Portici, 32:197-283.

ANT TAXONOMY

W. L. BROWN, JR.
Museum of Comparative Zoology, Harvard University

When the subject, title and dates for this survey were suggested to me, I could not but be struck by the coincidence of the century now complete with what I see as a major, if not entirely progressive, phase in the development of ant systematics.

If we begin the history of our myrmecological century at 1853, we find already existing a primitive chaos of Linnaean binomials scattered among "Formica" and a few other form genera. In the heyday of the two-line Latin diagnosis, beginning with Linnaeus in 1758, many workers in the general field of insect taxonomy—Fabricius, Latreille, Westwood, and others like them—accumulated a great many species of ants as mere incidents to their systematic outpourings. Only Latreille, and toward the close of the period, Nylander, gave the taxonomy of the ants more than a passing glance.

In the few years closely centered on 1853, three men, Gustav Mayr, Julius Roger, and Frederick Smith, entered the scene with publications focused more or less directly and exclusively upon ants. The study of the family would undoubtedly be farther advanced today had Smith never chosen to look at an ant, but this has been emphasized by so many authors already that I hardly need labor the subject. Creighton, in the historical introduction to his *The Ants of North America* covers Smith's work adequately and, in my opinion, with considerable restraint. At one point, he paraphrases Forel as stating "with his characteristic impetuosity . . . that neither Smith's species nor his types could be depended upon," and continues, "but while Forel's annoyance is understandable, he obviously overshot the mark. It is only because of Smith's types . . . that Smith's work was saved from oblivion." For myself, after considerable experience with Smithian species and Smithian "types" in the British Museum, I can only side with Forel on this question. Smith himself, and a few of his contemporaries and successors in the British Museum, had a genius for mistranscription, label-switching, and outright substitution or loss of specimens that has seldom if ever been equaled in the history of entomology. While it is no longer necessary to add to the damnation of Smith's work, it is important that the authenticity of his types remain open to question.

Passing to Roger, we find a man of a different stamp. His publications are relatively few in number, but the descriptions are very thorough for his day. He had a remarkable eye for genera. He struggled, as did Mayr, with the confused inheritance from the Linnaean period and with Smith's descriptive atrocities, and he reduced a goodly share of the mess to ordered synonymic lists. In all his work, Roger showed caution and restraint in the face of the exciting bizarre novelties then appearing in Europe from the corners of the world.

In Gustav Mayr, we come to a truly great myrmecographer. While maintaining other interests, he gave his best attention to the ants. Like Roger's, his descriptions were meaningful and perhaps even more to the point. Mayr early tackled the most important problem then confronting ant systematics—the genera and higher categories. What needed doing then is obvious to us now largely because Mayr did it. Starting with the Palearctic fauna, and then taking on the exotics, he apportioned with great insight the known and new forms into the familiar genera we know today, carefully characterizing each genus as he went. Fighting to recognize and correctly place not only the tremendous backlog of old species but also the spate from Smith's activity, he nevertheless found time to describe a great many species with a clear sense of the significant characters and a conservative approach to intraspecific variation that present-day investigation is ever more solidly confirming as superior to the fine nomenclatural splitting practiced by most of his successors. Mayr's names largely stand today as steady reference points in the taxonomic maze.

About 1870, in the middle of Mayr's course, Emery and Forel started their prolific taxonomic careers. The parallels and divergences between their lives and work has been covered by Creighton. Both Emery and Forel began with modest and useful studies of the European fauna, and Forel completed studies of great importance in his early publications on the comparative anatomy of the gizzard, poison apparatus, and anal glands, recognizing most of the features still serving to distinguish the major subfamilies.

Forel, however, soon discovered the unlimited taxonomic possibilities of the vast collections of ants rapidly accumulating in Europe with the development of the colonial empires. His work on ants then largely settled down to a routine of descriptions of exotic collections, one by one, and the numbers of species, subspecies, and varieties bearing his name rose steadily into the thousands. Creighton's estimate of Forel's descriptive efforts, while largely critical, is surprisingly mild, perhaps owing to the relatively small role played by Forel in the description of North American Formicidae. Even this role, as repeatedly shown in the synonymy of Creighton's book itself, was not a particularly distinguished one. Creighton's claim that Forel described ants "with ability and distinction," and his estimate that "among the great number of new ants which [Forel] described comparatively few were synonyms" are concessions too charitable for me to accept without protest. After his promising start, Forel's taxonomic career was one protracted degeneration into ever more hasty, careless, and often pointless proliferation of new names. I doubt very seriously that the year 2053 will see as many as one half of the names proposed by Forel in good taxonomic standing. Forel undoubtedly had a highly developed intuitive knowledge of the distinctness and affinities of many of the ants with which he dealt, and it is myrmecology's loss that he did not often pause long enough in his headlong pursuit of new forms to make clear either their distinctive characters or their real relationships. Excessive hurry, looseness, and confusion are the obvious marks upon most of Forel's publication, and the pentanomial system his characteristic medium of taxonomic expression.

Carlo Emery approached Forel in numbers of species described, and surpassed him in genera. In his early years, he produced a number of very useful papers, now all but forgotten, in which dozens of names from the old *inquirendae* lists were hunted down and tucked safely into the synonymic structure. His descriptions were more pointed than Forel's, and usually much more precise; many of the abundant illustrations he furnished, while often inaccurate in detail, provide the best evidence as to what the species of Smith and Forel are really like. Emery spent a large part of his physically handicapped career in the attempt to revise, classify, and key the species, genera, and higher categories, and in his classic contributions to Wytsman's *Genera Insectorum* he produced a unified system, key, and complete catalogue of the ants—the most useful work published in myrmecology to date. With Forel, he followed the weird and wonderful pentanomial system, but utilized it with much greater moderation than did Forel when describing novelties. Emery worked well and conscientiously, but the flood of unreliable contemporary description hurried him too much and threw him off the track at important junctures in his classificationary labors. Curiously, and unlike Mayr, Emery seems to have expressed remarkably little criticism of the work of his contemporaries, even though the constant interchange of types with Forel, Santschi, Wheeler, and others must have alerted him to their inconsistencies. It was calamitous that these authors should have been allowed to publish so copiously and for so long without the critical check earlier exercised by Roger and Mayr on the work of Smith. Only late in his life does Emery seem to have realized the extent of the damage done, as is apparent in his angry but flagging attacks on feckless dabblers like Bondroit and Donisthorpe.

W. M. Wheeler entered the field in 1900, and within a few years produced the general text, *Ants,* still in use but badly outdated. Wheeler's taxonomic writings came thick and fast, and were similar in style and quality to those of Forel, except that they were more frequently accompanied by illustrations and keys and were often weighted according to biological information gained in the field. Wheeler's work, like that of Forel, declined seriously with advancing years. His best contributions to taxonomic myrmecology were, perhaps, his studies on ant larvae and his treatment of the Baltic Amber fauna.

The years following 1910 saw many specialists joining the rush to describe ants: Santschi, Ruzsky, Stitz, Viehmeyer, Karawajew, Bondroit, Donisthorpe, Crawley, Menozzi, Clark, and numerous others. Taken generally, their work is very disappointing, following as it does more or less faithfully the pattern of Forel in spirit and method. One looks in vain among the thousands of dubious names and useless descriptions published by these workers for a real sign of a developing critical approach, but all that meets the eye is "sp. nov.," "subsp. nov.," "var. nov.," punctuated very occasionally by an irrelevant figure or an unworkable key. The freshest works of the period are probably those of Arnold and Mann, based on material largely collected by themselves in relatively remote and myrmecologically unknown parts of the world, and produced as whole faunas with keys and figures.

The reaction to this depressing period of description for description's sake and increasing taxonomic irresponsibility was dreadfully slow in gathering strength. In the 1920's and 1930's, the center of myrmecological investigation began, almost imperceptibly at first, to shift from Europe, with men like Bruch, Gallardo, and Borgmeier in South America, Arnold in South Africa, and M. R. Smith and Creighton in North America concentrating more closely upon the native ants of their own regions. In the light of their field observations and careful collecting, the pentanomial system came under a severe strain, and at the same time there arose a feeling that the art of description had fallen to a very low state. Improvements in techniques of sampling, description, and illustration became general, in large part at the insistence of Kennedy, but it was not until the appearance, in 1942, of Ernst Mayr's *Systematics and the Origin of Species* that the stage was set for the loosening of the debilitating grip of the pentanomial system upon ant taxonomy. This grip was first broken for myrmecology by W. S. Creighton's *Ants of North America,* appearing in 1950, a book that not only applied Ernst Mayr's principles broadly to a large fauna but finally signaled an uncompromising shift to the critical, revision-minded, biological taxonomy we hope is here to stay. After three years, it seems certain that Creighton's book is having a resounding effect on taxonomic theory and practice around the world, and it is especially gratifying to note that the younger workers are approaching the study with a revisionary spirit.

Because Emery's and Wheeler's generic keys are based on an unsound system to begin with, and because they have been swamped by the description of the past thirty years, the outstanding need in general ant taxonomy today is a new and workable key to the genera and higher categories. This must be based on a new and sounder classification, which in turn requires *debridement* through wholesale synonomy at all systematic levels and a thorough survey of comparative anatomy, both external and internal, in the various ant groups. Modern generic revisions, thoroughly done, deserve and are now receiving high priority. A survey of the male genitalia is badly needed. A look at recent publications and work in progress today shows a response to these needs that is encouraging on the whole, and there seems to be no reason why the current gratifying trend should not continue. Because of their huge and readily available populations and their segregation into colonial systems capable of considerable manipulation, ants provide a marvelous kind of material for biological study. It would be a shame if the taxonomic picture were to remain so confused as to continue seriously to hamper their usefulness.

THE ACULEATE WASPS

Paul D. Hurd, Jr.
University of California, Berkeley

In any review of the work accomplished during a certain period of time what we really are doing is attempting to examine accumulated knowledge in the light of the present in order that we may from the empirical evidence project our lines of thought toward the future. It is helpful, therefore, to evaluate the nature of the work undertaken in the study of the aculeate wasps during the past century. Fortunately for the purposes of establishing a natural point of reference, Frederick Smith published between 1853 and 1859 a catalogue of the hymenopterous insects in the collection of the British Museum, which, in a measure, not only provided a summary of the knowledge of the known wasp fauna of the world at that time, but, more importantly, pointed up the nature of the investigations which had preceded this date.

Large areas of the earth's surface were unexplored. Those areas that had received the attention of the hymenopterist were so poorly known that even a guess as to their faunistic composition and relationship could not be safely hazarded. The classifications of earlier writers (mainly those of Latreille, Lepeletier, and Dahlbom) were to a large degree inadequate and failed to afford a true reflection of the nature and extent of the world wasp fauna. To be sure, the wasp faunas of certain major political districts, such as England, France, and Germany had received more intensive study and were accordingly considered comparatively well known.

Several important lines of investigation suggested themselves following the appearance of the catalogue. Perhaps paramount was the realization that much material would be needed from Africa, Asia, Australasia, and the New World before a better understanding of the world wasp fauna would be forthcoming. Study of materials from the more poorly explored regions of the world suggested that much revision of ideas concerning relationship, distribution, and biology would be necessary. Consequent on these needs a greater effort to acquire faunal representatives from the large biogeographical regions of the earth was manifested in the increasing number of scientific expeditions. So remarkable were some of the discoveries in foreign lands that travelers and voyagers would return with tales of the gigantic sizes of the wasps.

From the 1850's until after the turn of the century the results of many of the exploratory expeditions were reported upon. The work of this period largely centered about the description of the material acquired and was usually in the form of large faunal works covering continental or subcontinental regions. Noteworthy contributions on this scale were made by André in Europe and North Africa (1882 *et seq.*), Ashmead in Hawaii (1901), Bingham in India (1897–1913), Cameron in Central America and the Orient (1888 *et seq.*), and Cresson (1867 *et seq.*) in North America. Toward the end of the nineteenth century an important deviation in the type of treatment occurred. Faunal studies began to be reduced in geographic scope. The revision or monograph of various categories usually of generic or familial level became more popular and provided a better method of analyzing and making known the composition of the better-collected faunal districts of the world. As each increment of information of a particular group or region was added to the fund of knowledge, the total biogeographic picture commenced to emerge.

In 1882 Alexandro Mocsáry published a comprehensive world list of the literature pertaining to the order Hymenoptera. This was followed a few years later by the appearance of Dalla Torre's *Catalogus Hymenopterorum* (1892–1902), a work which provided a stimulus for the more exhaustive monographic treatments which were to follow. More attention began to be directed toward accumulating more detailed information on the distribution and biologies of certain groups of wasps. Unfortunately little effort seems to have been made toward tying together all the available information on any one group. As new frontiers of the world were opened, largely through improved methods of transportation, so many new species were being collected that the taxonomist devoted a large share of his time to providing names.

In America, Thomas Say was chiefly responsible for initiating the descriptive phase in this country. Ezra T. Cresson (1863) brought together in his catalogue the described species of North American wasps. Cresson led the way in commencing an exhaustive study of the wasp fauna of North America. Similar investigations had preceded these—principally in England, France, and the German countries. The results of the European studies, as well as the influence of their workers, largely guided American thinking in matters of classification, phylogeny, and biology. By 1887 Cresson had presented a synopsis of the North American families and genera. At the turn of the century Ashmead re-examined the existing classifications and made an attempt to synthesize the existing knowledge relating to the phylogeny of the Hymenoptera. Other workers, such as Viereck in America, André in France, Cameron in England, and Bischoff in Germany, began to shape the broad outlines of the next twenty-five years of research on the wasps. In general, the lower categories, particularly on the generic level, were accorded a more thorough and virtually monographic treatment. This approach was, to be sure, closely correlated with advances in the related sciences and the improved technological equipment at their disposal.

Perhaps the most significant contribution to the knowledge of the aculeate wasps made during the present century has been the application of the principles stemming from the theory of evolution. While it is yet too early to determine the total effect this will have on the analyses and evaluations of problems dealing with biogeography and phylogeny, it is apparent that it will be profound. The present trend of study has assumed the form of synthesis of the various branches of knowledge so that the emerging interpretation of the aculeate fauna is directed toward reflecting the equivalency expressed in nature. This method seems best to achieve the ideal representation of the facts concerning the origins, phylogenies, ecologies, and the role of the wasps in nature.

In order to accomplish this interpretative representation it might be well first to re-examine more closely the present outlook on the basis of the probable world aculeate fauna. The recent catalogue of Nearctic Hymenoptera lists approximately 3,500 species and infraspecifics from an area representing nearly one-sixth of the earth's surface. Allowing for compensating changes in status, synonymy, and description of new species, as well as taking into consideration the relative ecological unequalness of faunas there are probably no more than 20,000 species of aculeate wasps inhabiting the surface of the earth. A figure of 15,000 species is more likely nearer the actual number, especially when infraspecific categories are taken into consideration. At first glance this figure seems small and suggests the possibility that at least certain main aspects of the study of the total world aculeate wasp fauna may soon be realized. This is particularly encouraging, for if we multiply 15,000 fourfold in an attempt to gain an appreciation of the principal developmental stages requiring morphological description alone, the chore ahead of us seems proportionately greater. Compounded to this arithmetical evaluation of extrapolated progress are those intangible aspects of the study which involve the fields of evolution, physiology, economics, and so forth, which, if reduced to a numerical power of 15,000 suggest an almost hopelessly astronomical figure—indeed one unobtainable in the life expectancy of the earth if presently employed methods of research and recording remain essentially the same.

The studies of the past century have provided us with a fund of knowledge—largely unsynthesized and scarcely subjected to interpretation—a basis, as it were, for theoristic advances in thinking and methodology so as to guide us in our ideal representation of the world wasp fauna.

THE APOIDEA

Charles D. Michener
University of Kansas

Taxonomy

The period 1853 to 1953 is particularly appropriate for a review of our knowledge of bees because in the year 1853 Part I of Frederick Smith's *Catalogue of Hymenopterous Insects in the Collection of the British Museum* appeared. This and the next part of the same work, published in 1854, dealt with the bees. In these publications a vast number of genera and species from all parts of the world were described. The first step in making known information on any group of organisms has always been the naming of the species involved. Numerous previous authors had started this process, so that most of the bee species of Europe were known by 1853 (see, for example, Kirby's *Monographia Apum Angliae,* 1802) and numerous species from elsewhere had also been described. The most comprehensive descriptive work prior to 1853 appeared in 1836 and 1841—*Histoire naturelle des insectes, Hyménoptères,* by Lepeletier de Saint-Fargeau. For their time both Lepeletier and Smith did excellent work, which has served subsequent bee students as well as can be expected.

From Smith's time to the present there has been a continuous series of authors describing species of bees from various parts of the world. In this country E. T. Cresson, of Philadelphia, described a great many bees, most of them in the years 1878 and 1879. Curiously, although Cresson lived and worked in Pennsylvania, most of his studies were based upon specimens brought back by numerous collectors in the West, for the scientific exploration of western America was in full swing in Cresson's time. Many of the bee species which could be collected in Philadelphia itself went undescribed during Cresson's activities and it remained for Charles Robertson to discover and name them in Illinois, mostly during the last decade of the last century and the first decade of the present one.

Probably because of the activities of Cresson and Robertson in this country and of l'Abbé Provancher in Quebec (many of whose species were incorrectly placed generically and still remain to be elucidated), European authors avoided work on North American forms after Smith's time. They studied material from all other parts of the world, and H. Friese in particular described thousands of species from all faunal regions except the Nearctic. His work extended over a very long period, at least from 1891 to 1935. Friese's counterpart in America was T. D. A. Cockerell, who first published on bees in New Mexico in 1894 and whose last work, on bees from Honduras, appeared in 1949. During this long period Cockerel described bees from all parts of the globe, and he himself collected them in many countries.

In addition to the publications of these workers who have studied bees from all parts of the world, notable contributions in collecting and naming bee species have been made by a number of students whose interests or opportunities have been more localized, for example Tarlton Rayment in Australia, E. L. Holmberg, Padre J. Moure, and C. Schrottky in South America, and P. H. Timberlake in California. Others have specialized on certain groups of bees, and have often contributed more of lasting value than those whose work has been of a faunal nature. Examples are H. J. Franklin (Bombini), T. B. Mitchell (*Megachile*), P. Blüthgen (Halictinae), and H. F. Schwarz (Anthidiini and Meliponini).

The result of all this activity has been a very large number of described species of bees. In the recent catalogue of *Hymenoptera of America North of Mexico* by C. F. W. Meusebeck *et al.*, 3,285 species and subspecies of bees are listed. Some of these will prove to be synonyms, but at least as many new ones will probably be described. Assuming that there may be 4,000 species in the entire North American continent and that the other major continents (South America, Eurasia, Africa) average 4,000 additional species each, while in Australia and insular regions another 3,000 species exist, we reach a total of 19,000 species. This is remarkably close to an estimate of 20,000 made many years ago by Friese.

Phylogeny

As large numbers of bee species were described, increasing attention was given to their relationships and to the manner in which they may be grouped in a classification. Earlier authors (e.g., Friese in 1895, W. H. Ashmead in 1899) arbitrarily divided bees into those which are parasitic and those which are not. The resulting classifications were highly artificial for they separated such obviously close relatives as *Bombus* and *Psithyrus*.

An entirely new and carefully considered classification of bees was proposed by Robertson, a Carlinville, Illinois, schoolteacher and botanist, in 1904. Robertson observed that the seventh abdominal tergum of many female and the eighth of many male bees bears a flattened, bare, margined pygidial plate. He believed that the presence or absence of this plate was a primary character dividing bees into two great natural groups. In fact, he went so far as to suggest that the pygidialate and apygidialate bees might have arisen from pygidialate and apygidialate specoid wasps, respectively. This classification had many merits but unfortunately Robertson, working with a limited fauna, did not realize that the pygidial plate could be independently lost in various groups.

Börner devised another classification in 1919, based primarily on mouthparts. Like the other classifications which utilize chiefly one set of characters, this resulted in some artificial arrangements.

A serious attempt to use all available characters was made by the present author in 1944. The result was a classification quite different from previous ones. It is to be hoped that as more characters are discovered and utilized, this classification will be modified to reflect the added knowledge thus obtained.

Bionomics

Most students of bees have been interested in bionomics of these insects. That a considerable amount of information on this subject was available for European species a century ago is shown by leafing through Part I of F. Smith's *Catalogue of British Hymenoptera in the Collection of the British Museum* (1855). Subsequent work has mostly been done in Europe, with German workers taking the lead in work on social Halictidae, Italian workers (especially Guido Grandi) on larval characters, with individuals of all principal nations contributing papers on nest-making and habits of various groups. Outstanding among students in this field was Malyshev. In America work on wild-bee biology has lagged almost until the present time, although several workers are now interested in such studies.

The importance of bees in cross pollination of various plants has been long understood, but only within the last fifteen years has the superiority of certain solitary forms over the honeybee for pollination of some crop plants been realized. This realization has provided a stimulus to the study of bionomics and several persons are now investigating these matters in the hope of solving practical pollination problems.

Some groups of bees of special interest for various reasons have received a great deal of attention. Outstanding, of course, is the honeybee, upon which much has been written. No discussion of this sort would be complete without mention of the famous studies by von Frisch, still under way, on the behavior and sense physiology of this insect. Another major group of social bees, the Meliponini, has received considerable study, for example from von Ihring in Brazil and more recently from H. F. Schwarz in this country and Warwick E. Kerr in Brazil.

The Future

The lines of investigation which now seem important for further study among bees are numerous. For example it seems certain that among the Halictidae every gradation between solitary and thoroughly social forms will be found and that studies of this grading series will shed light on the steps in development of social organization and the forces acting to cause such development. Further comparative studies will shed a flood of light on the evolution of instincts. Morphological studies of many sorts will provide further information on phylogeny, which is needed to verify or alter the present classification. Studies of such matters as parallelisms, orthogenesis, and the like can then be approached on a sounder basis. Biosystematic studies of all groups will add to our general knowledge of bee species, their ecologies, and their evolutionary and distributional patterns. In this connection a matter of special interest concerns pollen-collecting habits. Many species, termed polylectic, collect pollen from all sources; others, known as oligolectic, from only a few related species of plants. The evolution of this specialization, or the general problem of host specificity, can well be studied among bees for every intergrade between oligolecty and polylecty exists within numerous genera. These are merely some of the biological problems upon which bees may well provide information and upon which the present author and his students and associates hope to work. We trust that others will help, for there is work enough for many. Some will prefer to work on quite different problems, for example, pollination, sense physiology, and so forth.

One of the great troubles with most entomological papers is that they are written to be read by only a very few specialists. They provide a mass of minutae and few generalizations. Let us hope that more and more entomologists will attack and solve, through the insect groups in which they specialize, problems of general biological interest. Too many gather the needed data and are content to publish them without analysis, ignorant of or indifferent to the biological principles to which these data may contribute.

DIPTERA

Charles P. Alexander
University of Massachusetts, Amherst

As at present known, the Diptera or two-winged flies comprise the fourth largest order of insects, with approximately 85,000 described species, which possibly is not more than some 20 per cent of the total number in existence. Some of the better known countries and states have species of Diptera about as follows: Great Britain, 5,200; United States, 16,700; New York, 3,615; New England, 3,325; Michigan, 3,235.

Various classifications of the order have been proposed, the most recent by Hennig (1948) which separates the Diptera into two suborders, Nematocera, with sections Bibiomorpha and Culicomorpha, and Brachycera, with sections Tabanomorpha and Muscomorpha. A widely accepted arrangement, which is followed in this paper, divides the order into two suborders, the Orthorrhapha with two series, Nematocera and Brachycera, and the Cyclorrhapha with three series, the Aschiza, Schizophora, and Pupipara. In the following brief account, the leading events and many of the outstanding workers are indicated, together with significant dates of publication. Complete references may be checked in Hagen's *Bibliotheca Entomologica, The Zoological Record* (1864–date), and in other standard works.

First Period, 1758–1853

Linnaeus (1758) recognized only ten genera of Diptera, with no distribution into families, and including only 188 species. These genera in their exact arrangement and with the number of included species are as follows:

Genus	*Species*	*Genus*	*Species*
220. Oestrus	5	225. Empis	3
221. Tipula	37	226. Conops	6
222. Musca	100	227. Asilus	12
223. Tabanus	12	228. Bombylius	3
224. Culex	6	229. Hippobosca	4

Virtually all of the species were from Europe and chiefly from Sweden, with a very few from North America. That Linnaeus had no idea of systematic interrelationships is shown by his separation of the two Nematocerous groups, *Tipula* and *Culex*. Linnaeus' outstanding entomological student, Fabricius, greatly increased the number of species, both from Europe and abroad, and in introducing his so-called Cibarian system of insect orders, based on a study of their mouthparts, proposed the ordinal name Antliata to replace the Linnaean term Diptera, a suggestion that found little or no acceptance among later workers.

In 1800 there appeared a highly controversial paper by Meigen, the "Father of Dipterology," followed (1803–1838) by a series of notable works by this same student. Toward the end of the period several workers appeared, including Macquart (1838–1855) and Wiedemann (1819; 1828–1830), whose principal publications were on exotic Diptera, then becoming available in some numbers through various scientific expeditions. Other taxonomists included Curtis (1824–1840), Fallén (1814–1825), Haliday, Latreille, Robineau-Desvoidy (1830), Say, Schellenberg (1803), Stephens (1828–1846), and, toward the end of the period, Westwood (1839–1840), Zetterstedt, and Francis Walker.

In dipterous morphology, important basic work was done by Latreille (1825), who proposed terms such as prothorax, mesothorax, and the like, and by Audouin (1824–1832) who further refined the terminology of the thorax, giving us such familiar terms as scutum, praescutum, scutellum, episternum, and many others. In biology and life histories, the early studies by Swammerdam were carried forward in the notable works of De Geer and Réaumur. The first general textbooks on entomology were prepared by Burmeister, Kirby and Spence, and Westwood.

Second Period, 1853–1903

The close of the preceding period and the virtual end of the belief in "fixity of species" with the publication of Darwin's *Origin of Species* (1859), introduced a new and vigorous epoch. The pre-Darwinian belief resulted in an almost incredible synonymy in the order, as exemplified in an extreme instance in the posthumous work of Robineau-Desvoidy (1863), wherein the common parasitic fly, *Tachina vulgaris* Fallén, was redescribed no fewer than 245 times, the supposed species being distributed in five different genera!

In 1853, museums and collections containing Diptera were generally small and scattered. There was not one in the United States except the small Harris collection in Boston. In Europe, the leading collections were in London, Oxford, Paris, Leningrad, and Vienna. This neglect of the order was destined to be changed in an almost dramatic manner following the arrival in America in 1856 of Baron Osten Sacken, "Father of American Dipterology," who served as Secretary of the Russian Legation in Washington until 1862, and as Russian Consul General in New York from 1862 to 1871. Osten Sacken himself was one of the most accomplished students of the order, but served an even more important function in providing ample materials of North American Diptera for the study of Hermann Loew, outstanding systematic dipterologist of the period. Loew described as new some 1,350 species of North American Diptera, chiefly in a series of ten reports, or centuries (1861–1872), each including one hundred species. The combined Loew–Osten Sacken collections, now preserved in the Museum of Comparative Zoology in Cambridge, Massachusetts, comprise the most important basic series of flies in America.

Other outstanding European students of Diptera who were most active during this period included Becker, Bellardi, Bergenstamm, Bergroth, Bigot, Bonsdorff, Brauer, Dziedzicki, Egger, Gerstaecker, Giglio-Tos, Girschner, Jaennicke, Karsch, Kowarz, Lioy, Meade, Mik, Pokorny, Portschinsky, von Röder, Rondani, Rübsaamen, Schiner, Schnabl, Stein, Strobl, Winnertz, van der Wulp, Zeller, Zetterstedt, and various others. The outstanding major works of this group included Brauer und Bergenstamm's *Die Zweiflügler,* 7 parts (1880–1894), Rondani's *Dipterologiae Italicae Prodromus,* 8 volumes (1856–1880), Schiner's *Fauna Austriaca, Diptera* (1862–1864), and Zetterstedt's *Diptera Scandinaviae,* 14 volumes (1842–1860).

In North America, in addition to the work of Loew and Osten Sacken, this period marked the initial activity of Coquillett, Johnson, and Williston. Leading workers in South America included the Lynch Arribálzagas and Philippi (1865). In Australia, a most outstanding figure was Skuse, whose eight principal papers on the Diptera of Australia (1888–1891) are of unusual importance. Virtually all other taxonomic work on exotic Diptera was accomplished by students in America and Europe, including Bellardi, Schiner, and van der Wulp.

In the fields of dipterous morphology, phylogeny, and biology noteworthy advances were made. The science of chaetotaxy was proposed and developed by Osten Sacken (1881), although the term "machrochaeta" had been suggested many years before by Rondani (1845). A major landmark was attained in 1883 when Brauer first demonstrated the importance of the larva in classification and used the nature of emergence from the pupa to furnish the primary division of the order into Orthorrhapha and Cyclorrhapha. Weismann (1864) published an outstanding paper on dipterous development. Our state of knowledge of embryology was indicated by Korshelt and Heider (1890–1892).

Pioneer work on the venation and morphology of the wing was accomplished by Adolph (1879), Amans (1885), Cholodkowsky (1886), and others. Loew and Schiner proposed their respective systems of venation in 1862. Significant work on the morphology of individual dipterous types was done on the blowfly by Hammond (1881) and Lowne (1890–1895).

The earliest work on fossil Diptera began at this time with the appearance of Loew's paper on the Amber Diptera (1850). He was followed by several other students including Brongniart (1878), Forster (1891), Giebel (1862), Heer (1849–1865), Heyden (1870), Meunier (1892–1917), Oustalet (1870), Novak (1877), Scudder (1890–1894), and others.

The first catalogues of Diptera, covering various regions appeared, including Osten Sacken (1858; 1878) for North America, van der Wulp (1896) for southern Asia, Reed (1888) for Chile, and others. An outstanding event of the period was the publication of Scudder's *Nomenclator Zoologicus* (1882). Important general texts include those of Comstock and Packard.

Third Period, 1903–1953

At the very end of the preceding period, the discovery that certain blood-sucking insects and other arthropods carried diseases of man and other animals. focused attention sharply on the various families of Diptera that might be involved, including the Psychodidae (*Phlebotomus*), Ceratopogonidae (*Culicoides*), Culicidae, Simuliidae, Tabanidae, and various muscoids, and including also, because of its habits, the housefly. There followed intensive work on all of these groups from every possible aspect. These initial studies led to the publication of monographic works on mosquitoes by Theobald (1901–1910) and by Howard, Dyar and Knab (1912–1917), as well as a multitude of other papers and reports on the group, chiefly by Blanchard, Coquillett, Cristophers, Dyar, Giles, Goeldi, Graham, Peryassu, and others of the earlier period, and by Barraud, Bonne, Bonne-Wepster, Costa Lima, Edwards, Evans, Lang, Lutz, Martini, Matheson, Newstead, Patton, Shannon, Taylor, Wesenberg-Lund, and others of the intermediate period. At a still later date, especially during and after the recent war, a host of younger students have almost completely revolutionized our knowledge of mosquitoes, particularly from the tropics. Similarly, in the other groups of blood-sucking flies above mentioned, many capable workers have advanced our knowledge far beyond that of most other groups of Diptera that are not of medical importance. It is a matter of regret that restrictions of space prevent the listing of such students.

In the field of general dipterous taxonomy, the period likewise produced numerous workers. Some of these, particularly in the earlier years when the number of described species was still not excessive, were able to study certain families for the entire earth, while others were able to name many of the common flies of a more restricted area. There remain only a few such broad students of the order and we definitely have entered a period when specialization seems required.

Among those students who have described species in both suborders of Diptera are the following: Abreu, Aldrich, d'Andretta, Austen, Pereira Barretto, Becker, Bezzi, Brunetti, Coquillett, Curran, Duda, Enderlein, Engel, Fairchild, Frey, Johnson, Knab, Lutz, Mackerras, Malloch, Matsumura, de Meijere, de Meillon, Pritchard, Séguy, Shannon, Shiraki, Stone, Strobl, Taylor, Verrall, Williston, Wirth, and some others.

Some of the leading workers on the taxonomy of the Nematocera include the following: Abonnenc, Alexander, Barnes, Borel, Brug, Causey, Damasceno, Dampf, Doane, Dyar, Felt, Floch, Fox, Freeman, Goetghebuer, Hertig, Hoffman, Holmgren, Ingram, Johannsen, Kieffer, Kitakami, Komp, Lackschewitz, Landrock, Lane, Lee, Lengersdorf, Lundström, Macfie, Mangabeira, Mannheims, Martini, Natvig, Parrot, Pierre, Riedel, Rogers, Rozeboom, Sasa, Satchell, Shaw, Smart, Theodore, Tokunaga, Tonnoir, Townes, Vargas, West, and many others.

The chief students of the Brachycera and Cyclorrhapha include among others: Aczel, Arias Encobet, Aubertin, Bau, Bequaert, Bromley, Brooks, Brues, Carrera, Cole, Collin, Cortés, Cresson, Czerny, Duda, Efflatoun, van Emden, Ferguson, Ferris, Fluke, Goffe, Hall, Hallock, D. E. Hardy, G. H. Hardy, Hendel, Hennig, Hering, Hermann, Hesse, Hine, Huckett, Hull, James, Karl, Kertész, Kröber, Lichwardt, Lindner, Lundbeck, Melander, Metcalf, Miller, Munro, Newstead, Oldenberg, Oldroyd, Olsuf'ev, Pantel, Paramonow, Parent, Patterson, Patton, Philip, Pleske, Reinhard, Ricardo, Ringdahl, Sabrosky, Sack, Schmitz, Schuurmans-Stekhoven, van Schuytbroeck, de Souza Lopes, Speiser, Stackelberg, Stein, Steyskal, Stuardo, Surcouf, Szilády, Townsend, Villeneuve, Zia, and many more.

Great progress was made in the study of dipterous morphology, biology (including genetics), and embryology. In morphology, outstanding work was accomplished by Crampton (1909–1943), Ferris and his students, and Snodgrass (1909–date). A detailed bibliography is provided by Crampton (1942). Studies of certain body regions include the head and mouthparts by Peterson, the ptilinum by Laing (1935), the thorax by Snodgrass and Young, the pretarsus by Holway, and virtually all structures of the body by Crampton. Detailed morphological studies of specific insect types include papers by Williams on the Tanyderidae, and by Bromley on the Tabanidae. In wing venation, the basic studies begun by Comstock and Needham at the close of the preceding period culminated in the major work by Comstock (1918). Modifications of the Comstock-Needham system were proposed by Alexander, Bromley-Shannon, Goffe, G. H. Hardy, Lower, Séguy-Vignon, and others. Recent important texts have appeared covering the general subject by Berlese (1909–1925), Comstock, Imms (1925), Tillyard (1926), and others; on morphology by Snodgrass (1935); physiology by Wigglesworth (1939, 1950); and embryology by Hagan (1951) and Johannsen and Butt (1941).

In biology, very numerous papers on the immature stages were published, these being summarized in full by Hennig, 3 volumes (1948–1952). Some of the more important works on dipterous biology included those of Alexander (1920); Chu (1949); Demerec, on *Drosophila* (1950); Fabre (1913); Johannsen, on aquatics (1905–1937); Malloch (1917); Melin (1923); Miall, Peterson (1951); Phillips (1946); Rogers (1926–date); Thienemann, on aquatics (1914–1921); Usinger and LaRivers, on aquatics (1948); Wood (1952), and many others.

In genetics, the importance of certain flies, especially *Drosophila,* and to a lesser extent *Sciara,* has produced an almost unparalleled amount of research by many students, including two Nobel prize winners, Morgan and Muller. Other leading workers are Bridges, Metz, Patterson, Sturtevant, Beadle, and others.

Research on fossil Diptera was stimulated by the appearance of the major work by Handlirsch, *Die Fossilen Insekten* (1906–1908). Particular attention was devoted to the Florissant and the Baltic Amber (Bernstein-Forschungen, 1929–), by Alexander, Andree, Brues, Cockerell, Edwards, and others.

Marked impetus was provided in the study of the order by the appearance of various catalogues, manuals, and faunal treatments.

Catalogues: The outstanding catalogue is Kertész, *Catalogus Dipterorum* (1902–1910), the seven volumes covering the world fauna but being completed only to the Cyclorrhapha Schizophora. Other catalogues covering more restricted areas include Aldrich (1905) for North America; Becker, Bezzi, Kertész, and Stein, 4 volumes (1903–1907), the Palearctic Diptera; Brunetti (1920), the Oriental region; Miller (1950), New Zealand; Wu (1940), China; Stuardo (1946), Chile. Still other catalogues treat individual families for limited areas.

Lists: Of great value are the various local lists that indicate the extent of the fauna in any given area. Among such are the list of the British Insects, by Kloet and Hincks (1945); New England Diptera, by Johnson (1925); New York, by Leonard (1928); North Carolina, by Brimley (1938); and others.

Genera Insectorum: This outstanding publication (1902–date) combines the systematic treatment to genera with a list of the world species. Several fascicles have appeared but the work is still incomplete, the authors of the published parts including Alexander, Bau, Brues, Edwards, Hendel, Johannsen, Keilin, Kellog, Kieffer, Kröber, Melander, Pierre, Séguy, Surcouf, and Theobald.

Faunal Treatments and Manuals: A large number of publications fall in the above broad classification. Manuals considering the North American fauna include Williston (1908) and Curran (1934). Townsend's *Manual of Myology,* 12 volumes (1934–1942) considers the muscoidean genera of the world.

Treatments for the major faunal regions include, for the Palearctic, Lindner's great work, *Die Fliegen der palaearktischen Region,* 8 volumes with numerous parts by many specialists (1923–date). Oldroyd, Freeman, van Emden, Smart, Collin, and others, the *Diptera* of the Handbooks of British Insects series, volume 9 (1949–date). Séguy, Pierre, Goetghebuer, Kieffer, and others, *Fauna de France,* "Diptera" (1923–date). Lameer, *Fauna de Belgique,* "Diptera" (1907). Hendel, Hering, Karl, Sack, and others, *Die Tierwelt Deutschlands, "Diptera"* (1928–). Verrall, *British Flies,* "Syrphidae" (1901), "Stratiomyidae" (1908). Lundbeck, *Diptera Danica,* 7 volumes (1907–1927). Stackelberg, higher flies of European Russia (1933). For North Africa and the Ethiopian region, Efflatoun's *Egyptian Diptera* (1922–); *Reports of the Ruwenzori Expedition, 1934–1935,* published by the British Museum (1930–date); *Exploration Parc National Albert, de Witte and Other Missions; Brussels* (1937–date). For the Oriental region, the *Fauna of British India,* "Diptera," by Brunetti, Christophers, Barraud, Senior-White, Aubertin and Smart, 6 volumes (1912–1941).

In the New World, the *Biologia Centrali-Americana,* "Diptera," by Aldrich, Osten Sacken, Williston, and van der Wulp, 3 volumes (1886–1903). A most important series of volumes on the Diptera of Patagonia and South Chile has completely revolutionized our knowledge of this critical region; 7 parts, several fascicles, by various authors (1929–1948). For northeastern North America, the important Diptera of Connecticut series, by various authors (1942–date).

Other faunal treatments that may be mentioned include the *Fauna Hawaiiensis, Diptera,* by Grimshaw (1901), and the *Insects of Samoa, Diptera,* by Collin, Edwards, Malloch, and others (1927–).

Periodicals: Periodicals devoted entirely to the Diptera include the *Encyclopédie Entomologique,* "Diptera," Series B, by Séguy, Surcouf, and many others (1924–1940); those restricted to the order in large part are the *Zeitschrift für*

Systematische Hymenopterologie und Dipterologie (1901–1908), Konowia (1922–1931), and *Insecutor Inscitiae Menstruus* (1913–1926).

Modern Control of Dipterous Pests: The Diptera are of economic importance chiefly through their attacking man and animals and by the transmission of various diseases, as discussed earlier. A further group of species destroy various crops, among such being certain gall midges, Cecidomyidae, as the hessian fly, pear midge, cloverseed midge, chrysanthemum midge, and others (Barnes, 1946–date); the fruit flies, notably the apple maggot, Mediterranean fruit fly, Mexican fruit fly, and many others; and a variety of pests that attack garden and forage crops, as the frit fly, cabbage maggot, and many others. Before the advent of modern synthetic insecticides (about 1945) a system of control had been established against most of these pests, based partly on chemicals, but also utilizing biological and cultural methods. With the discovery of DDT and other well-known chemical compounds, very effective controls for many of these pests were obtained and it appeared that for certain of these, at least, the problem of holding them in check had been solved. However, at the present moment it has become apparent that certain of these insects have built up a strong resistance to all such types of chemicals and it appears that it is only a question of time before we will have to revert, at least in part, to former methods of control. Such statements apply specifically to the housefly and mosquitoes but apparently it eventually will apply also to most if not all of the other forms against which such chemicals are now used.

The Future

The vast increase in our knowledge of the Diptera during the past century seems certain to continue in every field of study. As regards taxonomy, it is certain that far less than one half of the species in the order have been described and, as indicated previously, it seems very possible to me that perhaps only some 20 per cent may have been made known to this date. The airplane and other methods of modern transportation will enable collectors to visit the remote spots of the earth and the great museums will continue to grow apace. The value of the type specimen has become increasingly apparent and every possible precaution should be taken to safeguard such unusually valuable specimens against loss from fire, atomic destruction, or from any other cause. As an added precaution, wherever possible, such types should be photographed or so illustrated that there remains no possible question as to the identity of the species. As the number of described Diptera increases, students of the world fauna will of necessity be compelled to restrict their studies to individual families or perhaps even to lesser categories, such as genera. Already there are certain genera in the order with more than 1,500 described species, with many more awaiting discovery.

Until very recently work on the taxonomy of any major group of insects was possible only to students who were connected with leading museums or universities that possessed unusually complete library facilities. The development of the microfilm and photostat processes, with other methods of reproducing literature quickly and economically, has changed this picture and it is now possible to procure copies of papers in rare or otherwise virtually unobtainable publications by the microfilm process, thus enabling students to work while far removed from major libraries.

As the species of any given region become better known, more attention will be devoted to the study of their biology and ecology. Compared to the number of described adults, only a small percentage of flies are known in their early stages and most of these are in groups of medical or economic importance. Similarly, under the impact of the so-called "New Systematics," increased attention will be devoted to a critical analysis of supposedly valid species in relation to clines and infraspecific categories. This analysis will result in a reduction in the number of supposed species but should be compensated for by the discovery of still unknown valid species.

These are merely indications of some of the problems that must be considered in the future. A fascinating field awaits the young entomologist who decides to devote his life and energies to a study of the Diptera.

SIPHONAPTERA[1]

George P. Holland[2]
Systematic Entomology Unit, Division of Entomology, Ottawa, Canada

The fleas constitute one of the smaller orders of holometabolous insects. About 1,350 species and subspecies, belonging to approximately 200 genera, are recognized at this time.

In the adult stage, fleas are ectoparasites of mammals or birds. Their small size, the difficulty of collecting them (except for a few species!), and the lack of suitable techniques and equipment for preparing and examining specimens made them unattractive subjects for study a century or more ago. It is possible, too, that in those early times the sordid circumstances generally associated with fleas discouraged attention from potential students, who turned their talents to problems involving more aesthetic creatures. Ferris (1951) quotes Denny (1842) concerning lice, which were similarly regarded: ". . . the author has had to contend with repeated rebukes from his friends for entering upon the illustration of a tribe of insects whose very name was sufficient to create feelings of disgust." Certainly, by 1853, fewer than 30 specific names for fleas had been proposed, and of these only about 17 are now considered valid.

Linnaeus recognized only two species of fleas, the so-called human flea, *Pulex irritans,* and the chigoe, *P.* (now *Tunga*) *penetrans.* In the early nineteenth century, the familiar "domestic" species from European dogs, cats, rats, house mice, and chickens were described by Curtis, Bouché, Bosc d'Antic, Schönherr, and Schrank. A few species from endemic European moles, hedgehogs, bats, badgers, squirrels, and birds were named during this period also, as well as an

1. Contribution No. 3054, Division of Entomology, Science Service, Department of Agriculture, Ottawa, Canada.

2. Head, Systematic Entomology.

echidna flea from Australia, and a giant flea from northern Canada. By 1853, only two genera, *Pulex* and *Ceratophyllus,* were recognized and no general classifications had been attempted.

The first systematic account of the order was that of Kolenati (1863), who recognized eight genera. The more conservative Taschenberg recognized but five in his important work (1880), which was the standard reference on fleas at the end of the nineteenth century, when three outstanding students of the order made their appearance in the literature. These were Julius Wagner of Russia, N. Charles Rothschild of England, and Carl F. Baker of the United States. These men had a purely academic interest in the fleas, for in those days the role of these insects as vectors of plague and other diseases was not known. The effect of the attack by this trio, and by some lesser students, on the virtually untouched fauna during the next few years is well demonstrated by three world lists published by Baker over a ten-year period. In 1895 he listed but 35 species (actually, he missed a few), which he placed in three families and six genera. In 1904 he catalogued 134 species, and in 1905, as a result of "a most extraordinary activity among students of this group," supplemented this list by approximately 120 additional names, arranging the whole into eight families.

About this time, the association between fleas and the dreaded bubonic plague was proved in India. There followed immediately a tremendous increase of interest in these insects, and the few specialists available found their services much in demand. Baker ceased work on fleas in 1905, but Rothschild and Wagner continued to occupy leading positions. The former purchased specimens from collectors all over the world, and, in 1915, established a publication (*Ectoparasites*) that was devoted almost exclusively to papers on the taxonomy of fleas. Dampf of Germany published a number of papers that were particularly well illustrated for their time. Oudemans, the great Dutch acarologist, published papers on flea phylogeny, in one of which (1909) was proposed a subordinal division that was followed for many years and has been discarded only recently. The most outstanding student of fleas, the former friend and colleague of Charles Rothschild, is Karl Jordan, whose work on the order extends over half a century. First assisting Rothschild (illustrating many of the early Rothschild papers), then publishing jointly until the latter's death in 1923, and since then continuing alone, Jordan has described more species and exerted more influence on the development of a natural classification of these insects than any other individual. His nearest competitor was Julius Wagner, who left Russia after the revolution of 1917 to live in Yugoslavia. Shortly before his death, Wagner sold his collection to the Staatsmuseum in Hamburg and it is known that the larger portion of it perished when the museum was destroyed by bombing during World War II. Wagner described many genera and species and published a number of works on flea morphology as well as a catalogue of the Palearctic species and several papers on classification, of which the most important appeared in 1939. The framework of our knowledge of the fleas of the world is based largely on the works of Rothschild, Jordan, and Wagner.

The first half of the twentieth century has been a period of species description and discovery of new specific distinctions. In 1900, for instance, Rothschild drew, for the first time, attention to the taxonomic value of the terminal abdominal segments of the female, and to specific differences in the spermatheca.

Though important theories on phylogeny have been published and classifications have been proposed, no really satisfactory arrangement is yet available. The lack of agreement on relationships is well illustrated by the treatment of *Anomiopsyllus* and related genera, which in three major works on North American fleas published between 1942 and 1947 appeared in three different families. Jordan, of all students of fleas the most experienced and best equipped to propose a general classification, has not done so, except for a limited but nonetheless important contribution in Smart (1948, rev. ed.). This neglect was in part deliberate, Dr. Jordan being reluctant to embark prematurely upon so difficult a proceeding when new and unusual material was turning up continually all over the world. Nevertheless, it was his intention to prepare a monograph of the fleas of the world, but this was prevented by World War II. However, all is not lost, and G. H. E. Hopkins and the Hon. Miriam Rothschild (daughter of Charles) are now preparing a catalogue of the Rothschild collection largely according to Dr. Jordan's views on the phylogeny of the group. All students of Siphonaptera eagerly await the appearance of this work, which should provide the most acceptable classification yet developed.*

The flea fauna of many parts of the world is now fairly well known; that of North America is particularly thoroughly investigated, in part because of concern over sylvatic plague, which is the manifestation of *Pasteurella pestis* in wild mammals. There have been numerous short papers by various authors, and larger taxonomic works have been published by Ewing, I. Fox, Holland, Hubbard, and Traub, and a catalogue of literature by Jellison and Good. The fleas of western Europe are fairly well known, and a group of siphonapterists, led by Ioff, have made extensive contributions to the knowledge of fleas in the U.S.S.R. Bedford, deMeillon, and Hopkins have published on African fleas, Liu on those of China, and Cunha, Pinto, Guimarães, and others have made contributions from the Neotropical region. Sharif of India has made important contributions to morphology as well as to taxonomy, and Traub and Smit are currently publishing descriptions of fleas from many parts of the world. In 1946, two papers of the greatest value to flea students were published. These were Snodgrass's account of the skeletel anatomy of fleas, and da Costa Lima and Hathaway's catalogue to the literature on the order up to 1944.

F. G. A. M. Smit of the British Museum at Tring recently circulated a list of about sixty contemporary students of fleas. Less than a score of these are really active in flea systematics, and most work at the species level. It is to be hoped that a number of students will devote their efforts to considerations of evolution and phylogeny of these insects so that a firm classification may ultimately be achieved.

It is now pretty well conceded that the fleas are divisible into two major groups, usually considered as superfamilies, the Pulicoidea and the Ceratophylloidea. These in turn may be divided into about 50 or more fairly well defined natural groups of genera, the arrangement and constitution of which are the basis for much present-day disagreement. Related species and genera may be assembled fairly conveniently, but a number of cases of wrong association through superficial resemblances brought about by adaptation remain to be sorted out.

---

*The first volume (of five) of this work has been published (1953) since this manuscript was prepared.

But the relationship of the groups to each other and their arrangement as a series of families, or as a hierarchy of families, subfamilies, and tribes, poses more difficult problems.

The origin of fleas, too, remains obscure. There is virtually no fossil record. DeGeer first recognized them as ordinally distinct from other insects. Various authors would associate the fleas with, or derive them from Coleoptera, Diptera, Mecoptera, Trichoptera, or Hemiptera. Jordan (1950) presented a provocative paper at the Eighth International Congress of Entomology at Amsterdam, and proposed that a symposium on the origin of fleas be organized for the Ninth Congress. That their association with mammals is of long standing is indicated by the host-relations of some groups today: a special family of fleas on bats, for example, and the so-called helmet fleas, which appear to be associated with marsupials in the Neotropical and Australasian regions. Many fleas exhibit a high degree of host specificity, and it is clear that many evolutionary lines have died out with groups of mammals that have become extinct. Some relict species suggest, in tantalizing fashion, some of these losses to the flea student. The primitive sewellel (*Aplodontia rufa*), besides having a parasitic beetle and two aberrant species of mites, supports four species of fleas, three of which belong to monotypic genera (two of these genera might well be placed in special subfamilies) and the fourth species is the largest of its genus and perhaps the world's largest flea! The evolutionary picture is sketchy in the extreme and is complicated by numerous examples of convergence and host-transference, all of which make the study of flea phylogeny and host-relationship even more difficult.

FOSSIL INSECTS

F. M. Carpenter
Harvard University

Since students of insect paleontology are dependent on the discovery of insect-bearing deposits, progress in this field has lagged behind that of other aspects of systematic entomology. Investigations of a century ago were largely concerned with insects preserved in Baltic amber and the Solenhofen (lithographic) limestone in Bavaria, both of which had been known since the time of the Roman Empire. In 1853 the amber insect fauna was in the process of being described by G. C. Berendt (with the aid of Hagen and others), whose two-volume treatise (1845–1856) deserves to be ranked among the great classics on insects. Many Solenhofen insects had already been described by Germar (1842), who then (1853) turned his attention to Tertiary insects of Germany. The same year (1853), O. Heer published the last of his papers dealing with the Tertiary insects of Oeningen and Radoboj, the whole series of publications forming a volume of over six hundred pages. The Jurassic insects of England were being studied by J. O. Westwood (1854) and Carboniferous insects from the Saar Basin by F. Goldenberg, who established (1854) the extinct order

Palaeodictyoptera. The first general survey of fossil insects was published at this time by C. G. Giebel (1856), *Die Insekten und Spinnen der Vorwelt;* this was a systematic review of all known fossil insects.

Shortly after this, in 1865, S. H. Scudder published the first of one hundred thirty papers which were to appear on fossil insects before his death in 1910. His contributions were by far the most important in the field. Most of his descriptive accounts dealt with North American material but his more general treatises were world-wide in scope. Included among the latter were his *Classed and Annotated Bibliography of Fossil Insects* (1890); *Index to the Known Fossil Insects of the World* (1891); and *Systematic Review of Our Present Knowledge of Fossil Insects* (1890). His *Tertiary Insects of North America* (1890) is on a par with Berendt's work on amber insects mentioned above. The discovery of insects in the Carboniferous shales of Commentry, France, in 1875, led to a notable contribution by C. Brongniart, *Recherches pour servir à l'histoire des insectes fossiles des temps primaires* (1894), in which the first specimens of giant Protodonata were described.

Shortly after the beginning of the present century, Handlirsch's *Die Fossilen Insekten* appeared (1906–1908). This, another classic in entomological literature, had a profound influence on the ordinal classification of insects in general. His *Revision des palaeozoischen Insekten* (1919) and the posthumously *Neue Untersuchungen über die fossilen Insekten* (1938–1939) were hardly more than superficial reviews of the literature. The chapter on insect paleontology which he contributed to Schröder's *Handbuch der Entomologie* (1921) and which contained many highly imaginative restorations, is his best known work on this subject.

Although many other entomologists, in addition to Handlirsch, have published on fossil insects during the past fifty years, only four have made insect paleontology their major field of study. These are: T. D. A. Cockerell, who described a great many insects from Tertiary deposits in Colorado, belonging to nearly all orders; R. J. Tillyard, whose stimulating papers on Permian and Mesozoic insects and on insect phylogeny in general aroused the interest of entomologists in these subjects: A. V. Martynov, whose investigations on Russian material have added enormously to our knowledge of Permian and Jurassic insects; and F. M. Carpenter, who has been chiefly concerned with the Carboniferous and Permian insects of North America and with the evolution of insects in general. In addition, mention should be made of A. Lameere, who, although he published only a few papers on the subject, made a significant contribution to general aspects of fossil insects.

Many other entomologists, far too numerous to be mentioned here, have made significant contributions on the geological history of particular groups of insects. The following might be mentioned as examples only: W. M. Wheeler (ants), C. T. Brues (parasitic Hymenoptera and phorid flies), F. Meunier (Diptera), G. Ulmer (Trichoptera), C. P. Alexander (Tipulidae), H. F. Wickham (Coleoptera), F. M. Hull (syrphid flies), F. E. Zeuner (Orthoptera), G. Statz (Diptera), E. E. Bekker-Migdisova (Hemiptera), and B. B. Rohdendorf (Diptera). In addition, a number of paleontologists have dealt with the insects of certain formations, notably H. Bolton (Carboniferous of England), P. Pruvost (Carboniferous of Belgium), and P. Guthörl (Carboniferous of Germany).

At present our knowledge of Tertiary insects exceeds that of any other past geological period; that of the Permian is the next best known. Most needed, therefore, are collections from other periods, especially the Cretaceous, which is almost a blank, so far as insects are concerned. Revisional studies of previously described material by specialists in certain orders are also needed, as well as investigations on unworked material. The most extensive collection of fossil insects, comprising about 60,000 specimens (including the Scudder Collection), is contained in the Museum of Comparative Zoology. Other important collections are in the British Museum (Natural History), the Institute of Palaeontology in Moscow, the Muséum National d'Histoire Naturelle, in Paris, and the United States National Museum. The collection of amber insects, formerly housed in Albertus University at Königsberg and including about 100,000 specimens, was destroyed during the Second World War.

HERPETOLOGY

By KARL P. SCHMIDT
Chicago Natural History Museum

Expanding herpetology,[1] like a branching tree, underwent development in various directions in its new growth during the latter half of the last century and the first half of the present one, and even within any one of these branches there may be varied directions of interest that require some disentanglement. In the present historical essay I have not attempted any unified arrangement, but have followed the branches or the individual twigs of the tree of herpetology as they have seemed important or interesting.

Herpetology may be broadly interpreted as including every phase of biological studies in which identifiable species or higher groups of amphibians and reptiles appear, and is so interpreted here. Emphasis, however, is upon the history of description and classification of the existing world fauna, which involves the story of the exploration of the world for the several thousand species of amphibians and reptiles. Most of the rise of our knowledge of the extinct members of these two groups falls within the century 1850–1950, but this segment of our history cannot be elaborated in the present essay.

Emphasis on the field of systematics, the central trunk of our tree, carries with it an interest in the natural history of the amphibians and reptiles. Natural history I interpret as the less critical forerunner of a more critical science of ecology. Even without this modern development, the natural history of the creatures in question has the merit of affording a base for the popular and semipopular literature of herpetlogy, which brings its more seriously scientific studies into the domain of knowledge of the general public and gives school children a key to a segment of the zoological sciences. This department of herpetological literature is peculiarly rich and requires some attention in a historical review. In addition to systematics, geography, and general natural history, the principal developments in anatomy, physiology, embryology, and behavior are of major importance to a broad view of the history of herpetology. Finally, within each of the separate fields, historic interest focuses upon the personalities of the individuals who initiated fruitful directions of investigation or dominated them. The principal museums of the world have had pre-eminent roles in the growth of systematic studies and in the exploration of the world for new species. Thus the hierarchies and successions of the museum herpetologists become important. The fact that

1. Studies on amphibians are commonly combined with those on reptiles in the zoological subscience "Herpetology." These creatures compose respectively the class Amphibia and the class Reptilia, two of the major groups of backboned animals, which were long combined in the Linnaean class Amphibia. The animals in question, the salamanders, frogs, and caecilians (the living amphibians as now understood), and the turtles, crocodilians, lizards, snakes, and the tuatara (the existing reptiles), were all commonly lumped together as reptiles in the popular mind and, for that matter, still are. The zoological distinction between the Amphibia and the Reptilia, though fully established, had not yet been properly carried through in general works at the middle of the nineteenth century.

the museums introduce an element of nationalism, sometimes of nationalist rivalry, adds interest to the story.

The Era of Duméril and Bibron

A major summary of the field of herpetology, in ten volumes, marks the end of the first half of the nineteenth century. This is the *Erpétologie générale ou histoire naturelle complète des reptiles,* by Andre Marie Constant Duméril (b. 1764, d. 1860) and Gabriel Bibron (b. 1806, d. 1848), based largely on the collections accumulated at the Museum of Natural History in Paris. The first volume of this work appeared in 1934, and the last in 1854; after the death of Bibron in 1848, A. H. A. Duméril, the son of the senior author, aided with volumes 7 and 9. The tenth volume is an atlas of 120 colored plates. This work, still much referred to, gives a comprehensive scientific account of the reptiles in general (including the amphibians as the distinct order Batrachia), as to their structure and physiology as well as their systematics, together with an historical account of the literature of the subject, and this is supplemented by a general account for each of the principal orders recognized. One hundred and twenty-one species of turtles, 468 lizards (with which are included the crocodilians), 586 snakes, and 218 "batrachians" are described. The classification of the snakes foreshadows the more modern ones of Cope and Boulenger in being based on dentition; five equivalent groups are recognized, the Opoterodontes, the Aglyphodontes, the Opisthoglyphes, the Proteroglyphes, and the Solenoglyphes. The last four terms were to become current herpetological property, useful even when their systematic importance was seen to be less than at first thought. The work greatly multiplied the number of known families of snakes, recognizing no less than twenty for the nonvenomous forms.

The *Erpétologie générale* was the crowning work of a century of herpetological studies, during most of which the leadership in the field had lain with the French. Earlier comprehensive treatments of the amphibians and reptiles had been supplied by the various editions of the *Histoire naturelle* of Buffon and the *Règne animal* of Cuvier. As a summary of what was known of the herpetology of the world in 1850, the *Erpétologie* remains a work of major importance. A direct line of succession of herpetologists at the Muséum National d'Histoire Naturelle at Paris carries on from Constant and Auguste Duméril through Leon Vaillant, F. Mocquard, and Fernand Angel (who died in 1950), to Jean Guibé. The most notable achievement of these generations was the herpetological exploration and description of the French colonies, especially of the great and remarkable island of Madagascar.

The Dumérils were not left unaided at the National Museum in Paris after the death of Bibron. Marie-Firmin Bocourt, who came to the museum as *preparateur* in 1834 at the age of fifteen, became a competent herpetological artist as well as field collector. His first expedition was to Siam in 1861–1862; in 1864 he was placed in charge of the Mission Scientifique au Mexique et dans l'Amerique Central, an adjunct to the attempt of Napoleon III to establish a Mexican empire under the ill-fated Maximilian. The failure of the Mexican venture sent Bocourt to Guatemala and other parts of Central America. After his return in 1867 he devoted himself to the report on his collections of reptiles, and more especially

ERPÉTOLOGIE

GÉNÉRALE

OU

HISTOIRE NATURELLE

COMPLÈTE

DES REPTILES,

PAR A.-M.-C. DUMÉRIL,

MEMBRE DE L'INSTITUT, PROFESSEUR DE LA FACULTÉ DE MÉDECINE,
PROFESSEUR ET ADMINISTRATEUR DU MUSÉUM D'HISTOIRE NATURELLE, ETC.

EN COLLABORATION AVEC SES AIDES NATURALISTES AU MUSÉUM,

FEU G. BIBRON,

PROFESSEUR D'HISTOIRE NATURELLE A L'ÉCOLE PRIMAIRE SUPÉRIEURE DE LA VILLE DE PARIS;

ET A. DUMÉRIL.

PROFESSEUR AGRÉGÉ DE LA FACULTÉ DE MÉDECINE POUR L'ANATOMIE ET LA PHYSIOLOGIE.

ATLAS

RENFERMANT 120 PLANCHES GRAVÉES SUR ACIER.

PARIS.

LIBRAIRIE ENCYCLOPÉDIQUE DE RORET,

RUE HAUTEFEUILLE, 12.

1854.

Figure 1. Title page of the *Erpétologie générale*.

to the production of 95 of the 101 plates in the accompanying atlas. Since he illustrated many of the type specimens from other collections and other museums, this great work remains one of the basic sources for studies on the Central American region. The amphibian section, with twenty-one plates, is by Paul Brocchi, and the reptile section was completed by Mocquard, the last six plates being by Fernand Angel.

Another direction of interest in herpetological studies in France may be seen in the continued attention to the fauna of France itself. As this became well explored as to systematics and geographic distribution, there arose opportunity for detailed attention to problems of life history and behavior. Leaders in this important reorientation of interests were Fernand Lataste, most important in herpetological history as the mentor of G. A. Boulenger, and Raymond Rollinat, who will be remembered for his fifty-year-long interest in *La vie des reptiles* (1934). Partly as a result of the long history of technical herpetological studies in France, the popular and semipopular literature of herpetology in the French language is particularly rich.

In the decades following the appearance of the *Erpétologie général* the prestige of leadership in systematic herpetology passed from Paris to London and Berlin. At Berlin the scientific productivity of Wilhelm Carl Hartwig Peters (b. 1815, d. 1883) spanned three decades of active publication during his regime as Professor of Zoology at the University of Berlin and Director of the Zoological Museum. His career began with an important personal zoological expedition to Africa, the *Reise nach Mossambique,* which extended from 1842 to 1848. Like most of his contemporaries, he was equally interested in various groups of animals, often combining the descriptions of new species of mammals and amphibians, or of snakes and fishes, and describing collections from three or four of the continents in the same paper. After his return from Africa a steady stream of short papers, mostly descriptions of new species, came from his pen in every year until his last. The first of the five great folio volumes of the reports on the *Reise nach Mossambique* appeared in 1852, the last in 1882. Of these the volumes on mammals, fishes, and amphibians[2] were by Peters himself.

Great collections of fishes, amphibians, and reptiles were meanwhile accumulating at the museum of natural history in Vienna, where the leadership in ichthyology and herpetology had fallen to Franz Steindachner (b. 1834, d. 1919). Steindachner, though more eminent in ichthyology, founded an Austrian school of herpetologists. He joined the staff of the Naturhistorisches Museum in 1860, and his publications in herpetology continue from 1862 to 1917. His papers include, with numerous short notes and descriptions, the reports on the collections of the Austrian Novara Expedition (1867), and quarto papers on collections made by himself in Africa, southwestern Asia, Brazil, and the Galapagos Islands.

Before we return to the main thread of the development of herpetological studies (in London), other direct derivatives of the Paris school may be mentioned. The Russian Imperial Academy of Sciences, and the Museum of Natural History in St. Petersburg became centers of herpetological publication under the regime of Alexander Strauch (b. 1832, d. 1893). Strauch was born in St.

2. Boulenger remarks that Peters was the last important herpetologist to employ the Linnaean class Amphibia in its comprehensive sense, to include both amphibians and reptiles.

Petersburg, came to the Zoological Museum of the Imperial Academy of Sciences in 1861, and became its director in 1879. His papers (all in German) in the *Memoirs* and *Bulletin* of the Academy (1862–1892) included revisions of the crocodilians, turtles, and viperine snakes of the world. Strauch's successor in herpetological studies was A. M. Nikolsky, whose first paper appeared in 1886, with comprehensive accounts (in Russian) of the amphibians and reptiles of the Russian Empire in 1915–1918 (*Faune de la Russie*). Jacques de Bedriaga (Russianized to Yakov Vladimirovitch Bedryagha; born in 1854, publishing career 1874–1912) interested himself especially in the herpetology of the Mediterranean region, of Europe generally, and at last of Mongolia. His account of the frogs and salamanders of Europe, *Die lurch fauna Europas* (1889–1897), is a comprehensive treatment of the fauna, though it suffers by comparison with Boulenger's magnificently illustrated work on the *Tailless Batrachians* of the same region. Bedriaga's reports on the amphibians and reptiles of the Przewalski Expeditions to Central Asia amount to more than seven hundred pages (with parallel Russian and German text), and ten plates.

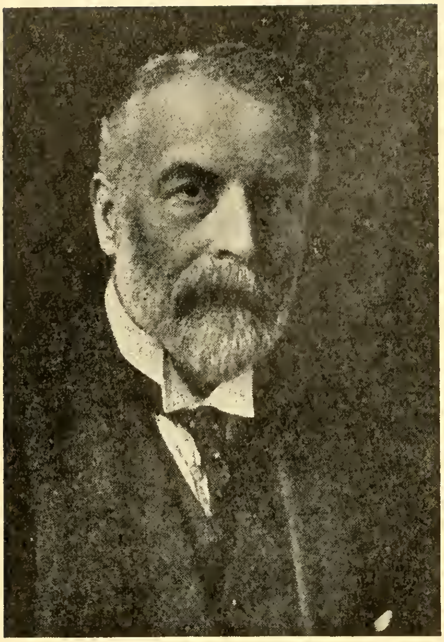
In Italy the wealth of lacertid lizards, whose suitability for pets in terraria has always been a source of herpetological interest in Europe, and the somewhat richer Mediterranean fauna in general, gave rise to an early and continuing interest in herpetology, and to one of the earliest elaborate accounts of a regional fauna. The "Amfibi" (both amphibians and reptiles) constituting C. L. Bonaparte's Volume II of his *Iconografia della Fauna Italica . . .*, (1832–1841), contemporary with the early volumes of the *Erpétologie générale,* depicted the amphibians and reptiles of Italy on 53 colored plates. The review of the Italian herpetological fauna was redone by Lorenzo Camerano between 1883 and 1891. The tradition of such national faunal works continues to the present day.

The director of the Museum of Natural History in Milan, Georg Jan (b. 1791, d. 1866), undertook the ambitious project of illustrating the snakes of the world. The coverage of this work was unhappily reduced by the refusal of the British Museum to lend its specimens to be drawn; but the 300 plates drawn and lithographed in uniform style by Ferdinand Sordelli (who completed the work after Jan's death) remain one of the monumental contributions to the illustration of the snakes of the world. The *Iconographie générale des ophidiens* was published in 50 *livraisons,* each with six plates (1860–1881).

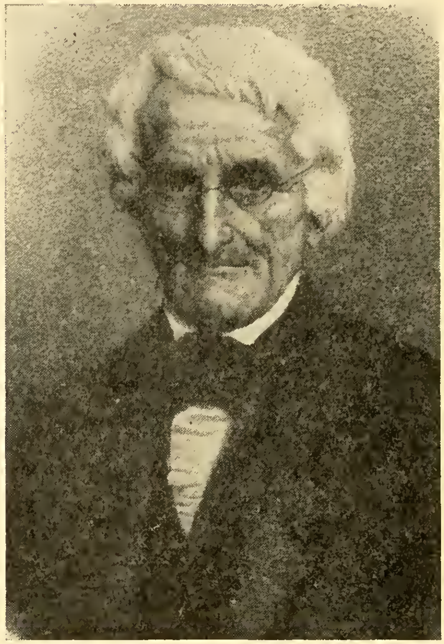
Opportunities for zoological exploration, often with governmental support, were presented in the foreign colonies of European nations, and these may dominate the herpetological interests of a national group. Such colonial exploitation is exemplified in the contributions of J. V. Barboza du Bocage (b. 1823, d. 1895), Director of the Portuguese National Museum in Lisbon, whose publishing career began in 1864 and was climaxed by his volume *Herpétologie d'Angola et du Congo,* published in the last year of his life.

The Era of Günther and Boulenger

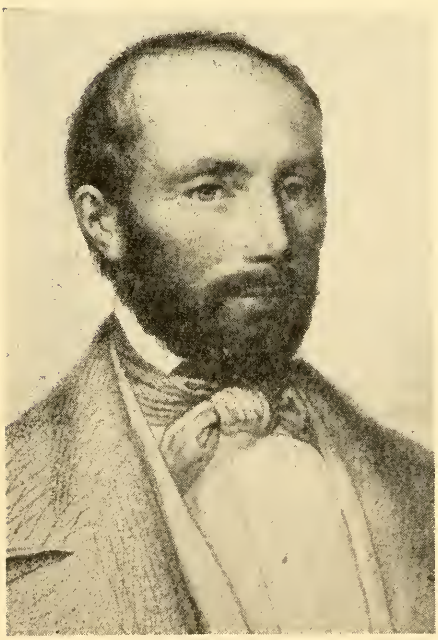
Reserving other developments in herpetology in various parts of the world and the early history of the field in the United States for later sections, we must turn to the dramatic transfer of leadership in the study of amphibians and reptiles from the Continent to Great Britain, and in particular to the British Museum



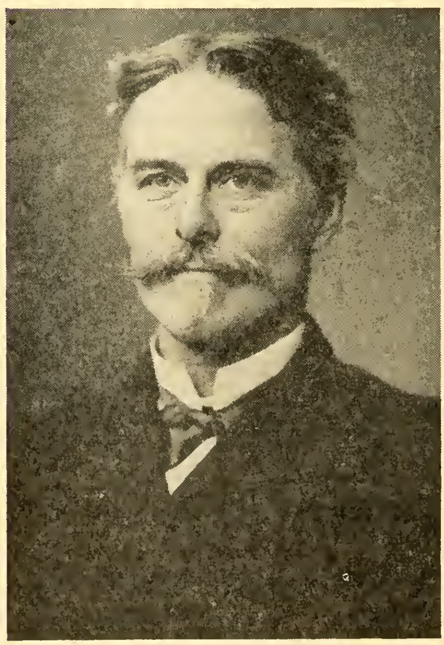
G. A. BOULENGER



A. M. C. DUMÉRIL



GABRIEL BIBRON



E. D. COPE

in London. In retrospect, the major turning point is discernible in the appointment of George Albert Boulenger to the curatorship of reptiles at the British Museum in 1880.

Studies on the amphibians and reptiles preserved in the British Museum had been greatly promoted by the voluminous but uncritical work of John Edward Gray (b. 1800, d. 1875), who began the tradition of published catalogues of the museum collections. Gray's publishing career (1825–1874) marks the rise in importance of two journals that became the principal media for the description of new forms—the *Annals and Magazine of Natural History* and the *Proceedings of the Zoological Society of London*.

Much of the most notable contribution made by Gray to herpetology was the choice of Albert Günther[3] (b. 1830, d. 1914) as his assistant in the divisions of ichthyology and herpetology, and, as it turned out, his successor as Keeper of Zoology. The young German (born at Esslingen, Württemberg), after taking holy orders in 1851 in the Lutheran Church, was diverted into a zoological career by the lectures of Professor von Rapp at the University of Tübingen. He took his degree as M.D. at that university in 1857, having meanwhile studied with the great anatomist Johannes Müller at Berlin and with Franz Hermann Troschel at Bonn, served at St. Bartholomew's Hospital in London, and written a book on medical zoology (published in 1858). In 1857 he accepted an assistantship offered by Gray at the British Museum, in which he was to catalogue the fishes, amphibians, and reptiles. By 1859 the great *Catalogue of Fishes* was under way, and the catalogues of Batrachia Salienta and of Colubrine Snakes were both published in 1858. His largest herpetological work was the folio *Reptiles of British India* (1864), published by the Ray Society.

Günther's most notable herpetological discovery was that the New Zealand tuatara is not a lizard but a living representative of an otherwise extinct order of reptiles, the Rhynchocephalia (1867). His contributions to ichthyology so much overshadow his herpetological work, that we tend to underestimate him as a herpetologist; but his greatest contribution to herpetology was, in his turn, his choice of successor, which fell to a young Belgian, George Albert Boulenger (b. 1858, d. 1937).

Before turning to the work of Boulenger and the Boulengerian era, it is necessary to note the work of the *Biologia Centrali-Americana*, and of John Anderson, the origins of which fall in the time of Günther. The herpetological share in the *Biologia Centrali-Americana* was important to the growth of the British Museum collections and affords an example, on a grand scale, of the effective aid of amateurs to museum work. The history of the *Biologia* is an extraordinarily pleasant story of a friendship between two Cambridge University students in the eighteen-fifties. Osbert Salvin and Frederick Ducane Godman were drawn together by a common interest in natural history, and their companionship led from wild-fowling in the Cambridge fens to the biological exploration of a quarter of a continent, resulting in the magnificent monument of the 63 quarto volumes of the *Biologia*. The volume on amphibians and reptiles (1885–1902), illustrated with 76 lithographic plates by the fine artists of the era, was prepared by Albert Günther.

Another notable herpetological career was that of John Anderson (b. 1833,

3. His full name, Albert Charles Lewis Gotthilf Günther, was usually so shortened.

d. 1900). With a medical degree from the University of Edinburgh, Anderson went to Calcutta in 1864. His arrival was fortunately timed, for the collections of the Asiatic Society of Bengal were then being turned over to the government of India. A new museum building was to be erected, and John Anderson was named Curator in 1865 and Superintendent a few years later. He retired in 1886, to live in London, and spent his winters in Egypt. While in India, Anderson took part in the two Yunnan expeditions, whose zoological results appeared in 1878–1879 in two quarto volumes, herpetologically important for their description of the remarkable turtle fauna of southeastern Asia.

John Anderson's career and interests fall sharply into an Indian and an Egyptian period. After his retirement he devoted hilmself (and no small part of his fortune) to the preparation and publication of the *Zoology of Egypt.* The quarto volume on amphibians and reptiles in this work (1898) is not only magnificent in format and illustration, but is one of the most competent and soundly useful of faunal works in the history of herpetology.

George Albert Boulenger, born at Brussels in 1858, exhibited a passion for natural history at an early age, and specifically for the study of amphibians and reptiles. During his student days at the University of Brussels he engaged in the identification of the materials in the Museum of Natural History (the Belgian National Museum) and came under the influence of M. Fernand Lataste, whom he addressed throughout his career with affectionate regard. His first paper, published at the age of nineteen, a revision of the iguanid genus *Laemanctus* with the description of a new species from the collections of the Brussels Museum, is already in such competent and scholarly form that it might have appeared forty years later, when he was the acknowledged dean of European herpetologists. He was made assistant at the museum in 1880, but very soon resigned, on the invitation of Dr. Günther to come to the British Museum to undertake a new edition of the catalogues of amphibians and reptiles, quite as Günther himself had been invited by Gray twenty-two years earlier. It is easy to see that it was the favorable impression made by the twenty papers published as the result of his work at Brussels that caused the young Boulenger to be invited to the most distinguished herpetological position in the world.

At the British Museum Boulenger immediately plunged into the work of revision of the classification of the amphibians, applying to the frogs and toads the system suggested by Cope in 1865, and literally bringing order out of chaos in this group. The volumes for Batrachia Gradientia (the salamanders) and Batrachia Salientia (the frogs and toads) appeared in 1882. Next came the three volumes for the Lizards, 1885–1887; the volume for Chelonians, Rhynchocephalians, and Crocodiles in 1889, and the three volumes for the Snakes in 1893–1896. Important contributions to the family classification were made throughout, and from the first, descriptions of the species *not* in the British Museum collections were included, so that these nine volumes constituted a summary of the world fauna for the classes Amphibia and Reptilia to the year 1896. Though his classification of the amphibians has required complete revision, his arrangement of the families of reptiles is essentially that current in 1950. Concurrently with the great series of catalogues, Boulenger published no less than 279 herpetological papers in scientific journals in the sixteen years from 1881 to 1896, in addition to a volume on the amphibians and reptiles of British India.

After completion of the catalogues, Boulenger continued with the descriptions of new species, reports on additions to the collection, and reports on individual collections from all parts of the world. His separately published subsequent works were the finely illustrated *Tailless Batrachians of Europe,* which reflects his principal contact with living amphibians and reptiles and his early interests in field observation (1896–1897); the compact little summary *Les Batraciens et principalement ceux d'Europe* (1910); the "Reptilia and Batrachia" in the *Vertebrate Fauna of the Malay Peninsula* (1912); the *Snakes of Europe* with its admirable introduction on snakes in general (1913); and the *Monograph of the Lacertidae* (1920–1921). Work on fishes in the British Museum began in 1887, and Boulenger thereafter continued to publish in both ichthyology and herpetology, with main interest on herpetology, much as Günther had worked in both fields, with emphasis of ichthyology. His total list of publications in scientific journals amounted to more than 875, of which 618 were on herpetological and 257 on ichthyological subjects. This is *without* enumeration of his more popular papers in *The Field, Country Life,* etc. This large list of publications reflects Boulenger's habit of rapid work, made possible by his having done the catalogue volumes, but this contained the seed of a weakness. His memory was phenomenal, so much so that he so readily recognized species that he had seen before that he was disinclined to check identifications made "through the glass"; and so great was his prestige among his colleagues that they also did not usually check his identifications further. When Clifford Pope and I were making a round of museum visits together in Europe in 1932, we could not help being amused at the dismay of some of our herpetological hosts when we questioned the determinations made by Boulenger on some casual previous visit, and insisted in our unbelieving way on having the jars opened so that we could examine the specimens more critically. Boulenger was not inclined to revise the keys for identification drawn up for the catalogues, and when these led him astray he sometimes described new species instead of making the revisions of his concepts that were indicated.

For all of Boulenger's mastery of the world fauna, he displayed little understanding of geographic distribution, and never alternated collecting and field studies with his work on preserved material in the museum. In still another respect his work was superficial—during the sixteen years of the production of the catalogue it was inevitably focused at the species level, and he displayed neither interest in nor understanding of the partition of species into subspecies, which has from the beginning, and of necessity, been based on more accurate knowledge of geographical and ecological relations. By no means an anti-evolutionist, the theory of evolution made astonishingly little impact on his thinking.

The great series of catalogues appeared before the organization of the International Commission for Zoological Nomenclature. Having already chosen those names that seemed best to him from a welter of early synonymy, it is perhaps scarcely surprising that Boulenger should have been casually indifferent to the new rules and codes. It is easy to understand also, how annoying this indifference was to those who, like Leonard Stejneger, took the new attempt to codify and regularize zoological nomenclature so seriously that they could quarrel in print over the omission or addition of an *l,* or over an elaborately complex method of determining the type species of a genus.

One of the most important accomplishments of the British Museum group was

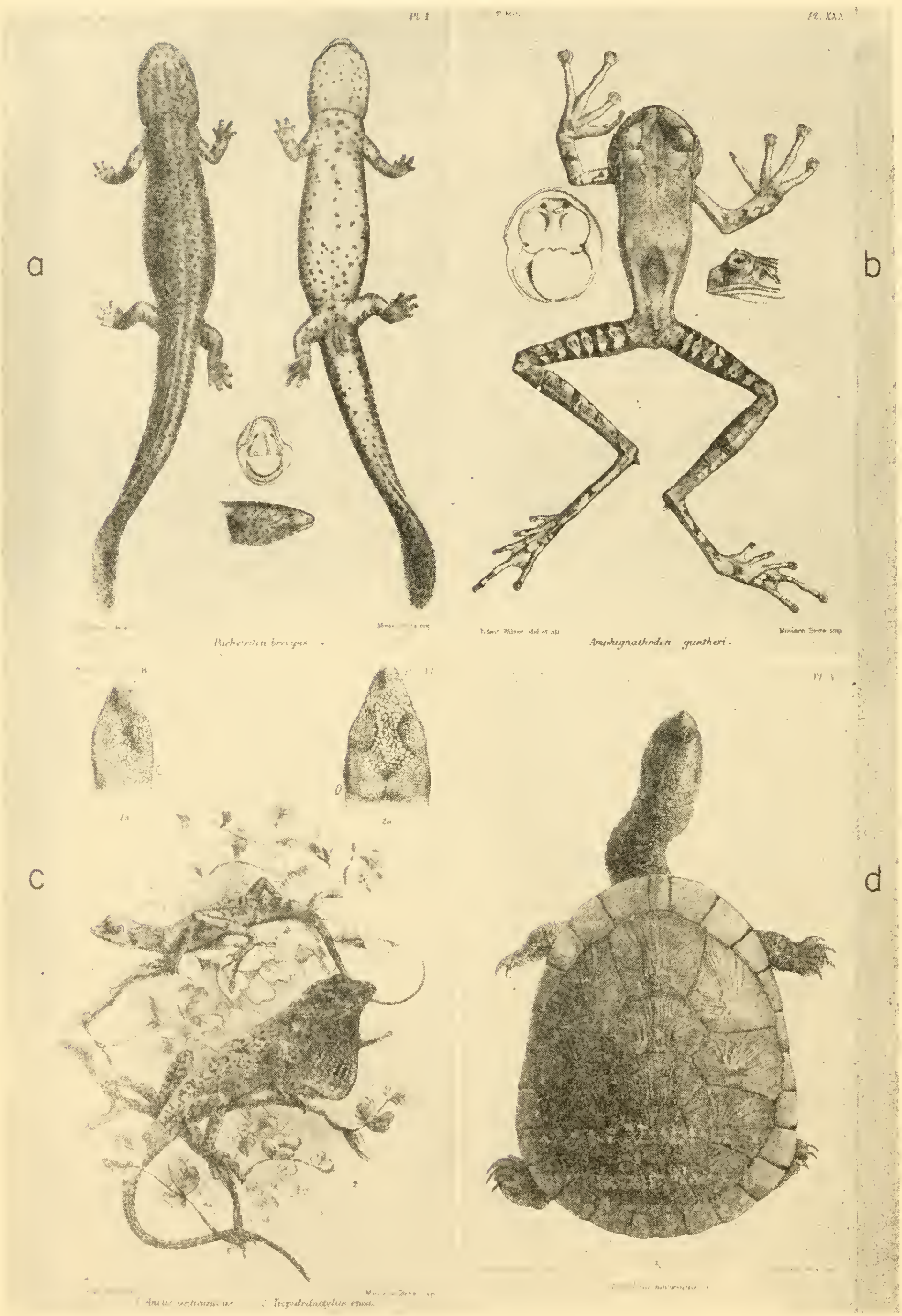


Figure 2. Specimen plates from Boulenger's *Catalogues: a.* From the *Batrachia gradientia*, 1882, *b.* From the *Batracha salientia*, 1882. *c.* From the *Lizards*, 1885. *d.* From the *Chelonians*, 1889. These show (in modern halftone reproduction) the kind of lithographic engraving that characterized all zoological illustration up to 1900.

the establishment of order in the rapidly expanding literature of zoology by means of the *Zoological Record*. This was founded by Günther in 1864; Günther himself contributed the sections for Amphibia and Reptilia from 1864 to 1872; from 1873 to 1879 they were done by A. W. E. O'Shaughnessy; and Boulenger took this field over from 1880 to 1914.

Boulenger retired from the British Museum and from herpetological studies on completion of forty years of service at the Museum, and returned to Belgium and to an early interest in the European wild roses. This was in 1920, and he lived for the seventeen years until his death in 1937 with scarcely a thought of herpetology—at any rate, with only three small additions to his list of papers.

It is easy to point to the defects of Boulenger's old-fashioned taxonomic work in herpetology and to sympathize with Stejneger, who was not only exasperated at Boulenger's lack of interest in nomenclatural changes, but was quite legitimately critical of the superficiality and carelessness of his work. There was to Boulenger's credit, however, the fundamental reform of the classification of the two great classes of vertebrates, which is so much now taken for granted that we tend to forget its importance; and there was the "merit of his defects," the fact that he did accomplish a complete review of the two great classes at the species level in the phenomenally short time of sixteen years; the two generations of his successors throughout the world have bogged down in the reviews of single families, and often enough made a life work of a genus. Systematic zoology needs its Boulengers.

The expansion of systematic herpetology from Duméril and Bibron to Boulenger, and to the present day, may be reflected in the numbers of living species known:

	Duméril and Bibron, 1854	*Boulenger 1896*	*Estimate, 1950*
Caecilians	8	43	70
Salamanders	58	130	240
Frogs	152	1146	2200
Turtles	121	219	265
Crocodilians	14	23	23
Lizards	454	1969	3140
Snakes	586	1639	2530
The tuatara	......	1	1

Lithographic Illustration of Amphibians and Reptiles

Great contributions were made to the illustration of the amphibians and reptiles of the world during the last half of the nineteenth century. This was the era of lithography. Able artists who had the patience to draw the scale detail of reptiles and the extremely skilled engravers on stone produced an extraordinary series of illustrations so accurate that they have not been surpassed, and need only the modern supplement of photographs from life. The art and technique of lithography flourished throughout Europe.

Among the artists available to Steindachner in Vienna Eduard Konopicky deserves especial mention for his ability to catch lifelike attitudes in lizards, as well as for the accuracy of his scale detail, which, it was said, made it unnecessary to examine the specimen. In England the expanding publications of the Zoological Society of London were richly illustrated with black and white and with colored lithographs. The great English herpetological artist of this era was G. H. Ford, who illustrated the numerous papers of Gray and Günther, including the *Reptiles of British India.* Of the 216 plates that illustrate Boulenger's catalogues, 78 are by P. Smit, 68 by R. Mintern, 42 by Mintern and Green, 19 by J. Green, 8 by Edward Wilson, and 1 by H. Grönvold. Smit's work illustrated the papers in the *Proceedings* of the Zoological Society of London between 1884 and 1900, and he produced forty of the fifty magnificent quarto plates in Anderson's *Zoology of Egypt,* the remaining ten being by H. Grönvold and J. Green. Green's colored lithographs continued to appear in the *Proceedings* in the first decade of the twentieth century, the last one in 1917. During the second decade of this century, lithographic illustration was superseded by the various photographic processes. The illustrations of the lithographic era had a curiously pleasing quality, in which scale detail was combined with shading, and the loss of this technique is a loss to zoological illustration. The illustrators of that period deserve a more extended essay in appreciation of their services to science.

The Boulengerian Era in Europe

The immediate usefulness of Boulenger's catalogues for putting in order the collections accumulated and accumulating in other museums, and the example of his numerous short faunal lists, fixed the style of herpetological publication for two generations in Europe. This Boulengerian era on the Continent continued the herpetological exploitation of the colonial empires, notably of the Netherlands Indies by a Dutch school[4] still in the shadow of the great Hermann Schlegel; of the Belgian Congo by Boulenger's successors in Brussels,[5] and of the German African colonies by a Berlin group.[6] None of these rose above an unthinking multiplication of morphological species. The synopses of the Amphibia Salientia in *Das Tierreich* by Nieden (1923) and Ahl (1931) do not rise above this level.

Typical of such active national herpetological exploitation of colonies is the somewhat later work of Guiseppe Scortecci, in Milan, and later in Genoa, on the expanding Italian colonial empire. His earliest papers (1928) reflect this interest, and one even suspects unrealized colonial ambitions in papers on the reptiles of Yemen. The Italian contemporary of Boulenger was Count Maria Giacinto Peracca (b. 1861, d. 1923), whose ample means enabled him to keep a terrarium on the scale of a large conservatory, in which Galapagos turtles wandered at will. His publishing career and association with the zoological museum of Turin extended from 1886 to 1917. His interests were wide, with a long series of papers on South American herpetology.

The Boulengerian era in Vienna included the colleagues and successors to Franz Steindachner. Friedrich Siebenrock made notable contribution to the anatomy and systematics of turtles (publishing career, 1892–1924). Otto Wettstein (son of the eminent botanist) will be most remembered for his detailed account of the anatomy of the tuatara in the Kükenthal *Handbuch der Zoologie* (1931). On the retirement of Wettstein, the division of herpetology at Vienna was

4. J. K. de Jong, Nelly de Rooij, P. N. Van Kampen, and L. D. Brongersma. Properly representative of more modern ecological field observation, Felix Kopstein (–1940) may be named with this group.

5. G. F. de Witte and Raymond Laurent.

6. Gustav Tornier, Fritz Nieden, Richard Sternfeld, Ernst Ahl, and Günther Hecht.

placed in charge of Joseph Eiselt. Franz Werner (b. 1867, d. 1939), long active as a teacher at the University of Vienna, was, perhaps unfortunately, *persona non grata* at the Natural History Museum in Vienna under the regime of Steindachner. Much of Werner's work is competent herpetology in imitation of Boulenger; his reputation is marred by a few papers in which well-known exotic snakes are described as new species and new genera. These are wholly incongruous with his technically competent general account of the Amphibia and the special treatment of the Apoda in the *Handbuch der Zoologie* (1930). His major contribution to herpetology is his two-volume account of the amphibians and reptiles of the world in the fourth edition of Brehm's *Tierleben* (1912–1913), which is of broad interest to zoologists in general.

An independent herpetological center grew up at the Hungarian National Museum at Budapest under the influence of Lajos von Méhelÿ (whose herpetological publications begin in 1890) and Baron G. J. von Fejérváry (first paper in 1910). Méhelÿ was naturally enough interested in the European herpetological fauna. For the lizards of the genus *Lacerta*, his ideas as to which were the primitive and which the derived forms differed sharply from those of Boulenger. It is somewhat surprising to find an extensive series of papers by this author on New Guinean and South American frogs. Baron Fejérváry, who was succeeded by his wife as curator of the herpetological collections, is known for his studies of the fossil varanid lizards and their relatives. Most of these papers are in German, some in both Hungarian and German. Since World War II Mrs. Fejéváry has been publishing in Hungarian without benefit of summary in another language.

There has been active interest in herpetology in the several Scandinavian countries since the times of Linnaeus. This is reflected not only in active work on the North European fauna, but in an interest in the amphibians and reptiles from foreign countries. Collections from individual travelers and from expeditions have accumulated in the museums and university collections of Sweden, Norway, and Denmark, throughout the Boulengerian and post-Boulengerian eras and have formed the basis for numerous reports[7] (mostly in English or German).

Oskar Boettger (b. 1833, d. 1910), equally known for studies in malacology and herpetology, made the Senckenberg Museum at Frankfort on the Main a center of herpetological studies. His papers reflect an influence quite different from the direct colonial interest of the national museums, and one characteristic of Frankfort, for the numerous correspondents who sent him specimens were businessmen with amateur interests in natural history, who took time to collect for him, and for the home town museum, in China, at the Lower Congo, in Madagascar, and in central Asia. Boettger's first herpetological paper is in 1869; but his catalogues of the collections in the Senckenberg Museum (1892–1898) place him clearly in the school of Boulenger. He contributed the account of the amphibians and reptiles, a volume of 826 pages, to the third edition of Brehm's *Tierleben* (1892).

The Modern Era of Herpetology in Europe

Boettger was succeeded at Frankfurt by Robert Mertens (b. 1894), who has been an active field student in the East Indies and West Africa, as well as in the

7. By Lönnberg, Andersson, Rendahl, and Volsøe, to name only a few.

West Indies and Central America, with a monumental review of the lizard family Varanidae (1942) and a general account of insular reptiles as notable contributions, in addition to the reports on his own expeditions. He falls sharply out of the Boulengerian school in *Die Amphibien und Reptilien Europas* (1928, 2nd ed. 1940), a check list drawn up on the plan of the check list for North America of Stejneger and Barbour, produced in collaboration with Lorenz Müller.

The Zoologische Sammlung des Bayerischen Staates, the repository of the Spix and Martius Brazilian collections, an independent center of herpetological studies, renewed active herpetological work with the appointment of Lorenz Müller (b. 1868) as curator of reptiles (about 1906). Müller was immensely stimulated by a zoological expedition to the region of the Lower Amazon in 1909; his background as a competent zoological artist, curiously enough, does not appear in his own publications. In 1932 he was joined by Walter Hellmich, who had returned from Chile with large collections and brought to herpetological studies the background of a training at the Zoological Institute of the University, thus again marking the end of the era of Boulengerian dominance in Europe.

Another German center of herpetological studies was created at Magdeburg by Willy Wollterstorff (b. 1864, d. 1943), to whom lifelong deafness seems to have been a stimulus rather than a handicap. After early paleontological papers he began to devote himself more and more to the salamanders, which are so richly represented in Europe, and which lend themselves so well to observation of habits in captivity. Wollterstorff is succeeded in these interests by students and colleagues in Wolf Herre (Kiel) and Günther Freytag (Berlin).

The continuing interest in the insular lizards of the Mediterranean Islands, at first mainly a matter of nomenclatorial rivalry, has been shared by most of the herpetologists of the European continent. Even as early as the 'seventies, Theodore Eimer (b. 1843, d. 1898) called attention to the problems of environmental effect and of the origin of species and subspecies. Papers by Wettstein, Müller, Mertens, and Eisentraut are written from the more modern viewpoint of an interest in speciation. The somewhat parallel insular phenomena in the West Indies and in the Gulf of California have long attracted American herpetologists. It seems proper to record the failure of one ambitious plan of attack on this problem in the West Indies. In conversations on West Indian herpetology between myself and G. K. Noble, which began in 1916 (and resulted in Dr. Noble's expedition to Hispaniola in 1922), we agreed that only direct comparison of living lizards, in good series, would be adequate to establish the degrees of differentiation from island to island; that preserved collections from different dates and scattered localities would not serve; and that only a special expedition in a suitably small vessel would answer our needs. When Gilbert C. Klingel appeared as volunteer aid in the Department of Herpetology, the matter was laid before him; and the result was the perfectly planned and completely disastrous voyage of the yawl *Basilisk* in 1930, the story of which is recorded by Klingel in *Inagua* (1940). The *Basilisk* was fearfully storm-beaten and piled up as a total loss on the reefs of Inagua Island in the Bahamas at the very beginning of her maiden voyage.

Boulenger so dominated his Continental colleagues that his influence among them persisted long after his retirement. Neither Boulenger nor his catalogues ever gained any corresponding respect in North America, which has produced its own school of herpetology.[8] It is remarkable, however, that Boulenger's influence should have disappeared so abruptly in London with his retirement; when his post became vacant, it was filled by a broadly educated young Cambridge graduate, H. W. Parker (1897–), who brought quite new ideas to his studies on the collection. His revision of the catalogue of the Amphibia Salientia was undertaken on a vastly more detailed and thoughtful basis, and thus has been carried through only the families Microhylidae (Boulenger's Engystomatidae) in *A Monograph of the Family Microhylidae* (1934), and through most of the Leptodactylidae. George E. Nicholls, a young British student at King's College in London, had made a noteworthy contribution to the classification of the Salientia in a little paper on "The Structure of the Vertebral Column in the Anura Phaneroglossa and Its Importance as a Basis of Classification" (1916). The significance of Nicholl's suggestions was more especially elaborated by the late G. K. Noble.

Miss Joan Proctor (b. 1897, d. 1931), to whom Boulenger refers (I believe with affection) as "mon élève," would perhaps have been his choice to succeed him at the British Museum. She studied with him and aided in the Division during his last four years at the Museum. Her somewhat precarious health prevented her being taken onto the Museum staff, and a place was found for her as the curator of reptiles in the Zoological Gardens of the Zoological Society of London. Her few herpetological papers give little clue to the extraordinary competence she brought to the planning and management of the new reptile house built at the Zoo under her regime. She thus has a secure place in the history of herpetology, in the large subject of the history of the keeping of amphibians and reptiles in zoological gardens, and in her relations with the British Museum group.

A most effective "research associate" had meanwhile appeared at the British Museum in Malcolm A. Smith (b. 1875). Dr. Smith had made a large personal collection of amphibians and reptiles, and engaged actively in herpetological studies, while attached to the Court of Siam as Court Physician.[9] On his retirement he continued these studies and greatly expanded them in the revision of the "Amphibia and Reptilia" for the *Fauna of British India.* The volumes for turtles and crocodiles (1931), lizards (1935), and snakes (1943) have appeared, in addition to the *Monograph of the Sea Snakes* (1926), which effectively brings one of the smaller families of snakes up to date from Boulenger's catalogue of 1896.

Emendations and additions to the *Catalogue of Snakes* were made by Colonel Frank Wall (b. 1868, d. 1950 of the Indian Medical Service, who had great opportunities to collect and study Indian reptiles. He interested himself especially in snakes and their habits in life, and in the treatment of snake bite. His series of accounts of Indian snakes, with splendid colored plates, "A Popular Treatise on the Common Indian Snakes" (in the *Journal* of the Bombay Nat. Hist. Soc., 1906–1919) was unfortunately never published in book form; he is known especially for his *Snakes of Ceylon* (1921) and for *The Poisonous Terrestrial Snakes of Our British Indian Dominions* (4th ed., 1928). It is something of a curiosity, more especially in a herpetological career that was essentially that of an amateur,

---

8. The treatment of the North American herpetological fauna is, in fact, one of the weakest features of the *Catalogues.*

9. See Malcolm Smith, 1946, *A Physician at the Court of Siam.* London: Country Life Ltd., 164 pp., illus.

that Colonel Wall should have dropped herpetological investigation and publication completely on his retirement in 1925.

The rather inflexible organization of the British Museum staff, which assigns a clerk to a Division, but does not envisage the advancement of a clerk to a curatorship, is in sharp contrast with American Museums where every office boy aspires to be director. It is thus gratifying to an American observer that J. C. Battersby (1901–), Clerk in the British Museum's Division of Reptiles, was at last placed in charge of the Division, since, when Dr. Parker was made Keeper of Zoology, the Trustees of the Museum refused otherwise to fill his vacated post in reptiles, apparently on the ground that he (Parker) could fill both positions. Mr. Battersby, meanwhile, has carried on the useful role of herpetological bibliographer for the *Zoological Record,* which, after Boulenger's last contribution in 1904, had been compiled by Sollas, Tate Regan, C. L. Boulenger, Joan Proctor, and Malcolm Smith.

Herpetology in North America

Herpetology in North America had made promising beginnings by 1850, and stood on its own feet in its exploration of the North American continent. *The North American Herptology* of John Edward Holbrook, published in two editions, with a multitude of emendations and separate printings of individual plates between 1836 and 1842, had established the North American region as a special field. The collections of the Academy of Natural Sciences in Philadelphia had become important, and had formed the basis for numerous herpetological papers in its *Proceedings.* In 1850 Spencer Fullerton Baird (b. 1823, d. 1887) became Assistant Secretary of the Smithsonian Institution, i.e., Director of the United States National Museum. Baird's interests ranged over the whole field of zoology, though certainly with herpetology as his last and most permanent love. The *Catalogue of North American Reptiles,* characteristically perhaps, carried no further than Part I (the snakes), was prepared jointly with the young Frenchman, Charles Girard (1822–1895), one of the able assistants attracted to Washington by Baird. Another of these was Robert Kennicott of Chicago, whose death in Alaska in 1866, at only thirty-four, was one of the calamities to North American zoology, and more particularly to the development of natural history in the Middle West. More important than his own writings in herpetology was Baird's indefatigable encouragement of the collecting of specimens for the rapidly growing scientific collections for what was to become the United States National Museum. He became the second secretary of the Smithsonian Institution (i.e., its Director) on the death of Joseph Henry in 1878 and in that capacity furthered herpetology still more by the program of publication of the new Museum, whose first *Bulletin* appeared in 1875, though the formal designation of the Museum as a separate entity came in 1876.

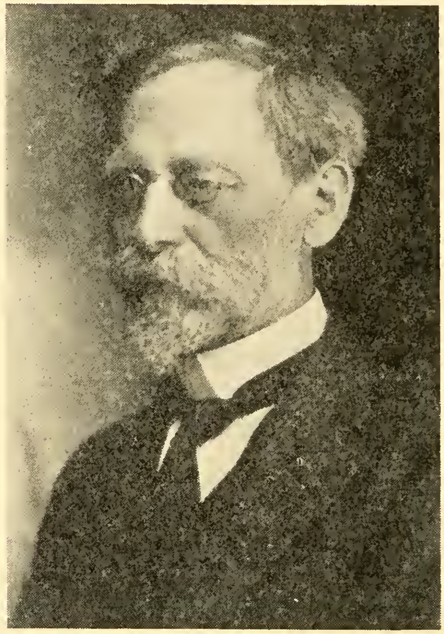
The importance of Baird in the history of American science, and perhaps especially to American herpetology, can scarcely be overemphasized. Together with the encouragement of collecting and his own reports on the growing collections, he furthered the careers and interests of the younger American zoologists of his day. In addition to his faithful collaborator Girard and the enthusiastic young Kennicott, there were W. H. Yarrow and finally the brilliant and independent Cope. We are fortunate to have a fine biography of Baird by his long-time associate in Washington, the malacologist W. H. Dall.

Baird's untiring efforts to promote the growth of the great museum he helped to found, and his unselfish furtherance of the careers of others left him less known to succeeding generations than was the brilliant but sometimes erratic Edward Drinker Cope (b. 1840, d. 1897). Like Baird, and like most other herpetologists of the last century, Cope worked in many fields and is remembered quite as much for his explorations and publications in paleontology and for his studies on fishes as for his contribution to herpetology. Some of his more solid accomplishments were herpetological. They include his discovery of the profound difference between the true frogs and the true toads in the anatomy of the shoulder girdle and sternum, which made possible the first real advance in the classification of the whole group of tailless amphibians. Museum specimens were long jealously guarded against dissection, and their classification, it was thought, should be sufficiently accomplished by the examination of external characters. Cope's discovery, which required the laying back of the skin of the breast in order to determine the classification of a specimen in hand, ran counter to museum practice. During his European tour in 1863, when he visited the Museum of Zoology of the University of Berlin under the guidance of the still conservative Wilhelm Peters, it is said that Cope carried an open penknife in his hand and surreptitiously examined the pectoral girdles of genus after genus of frogs that had previously been unknown to him. These he could then place correctly into the two great series Arcifera (for those with overlapping coracoid bones or cartilages) and Firmisternia, with the coracoids firmly anchored to a median sternum. His early paper "Sketch of the Primary Groups of Batrachia salientia" (1865) sets forth this cornerstone of amphibian classification (see especially, however, G. K. Noble, below).

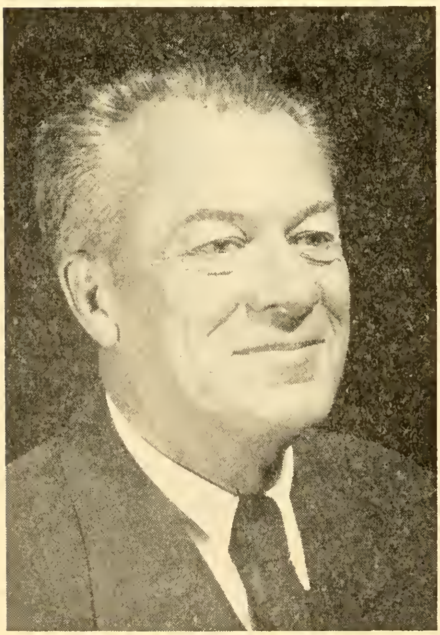
In addition to the continuous flow of small and large papers from Cope's pen, mainly in the *Proceedings of the Academy of Natural Sciences of Philadelphia* and the *Proceedings of the American Philosophical Society,* Cope's major herpetological works were *The Batrachia of North America* (1889) and *The Crocodilians, Lizards, and Snakes of North America,* which appeared in 1900, three years after his death. Both works incorporated large blocks of manuscript descriptions left by Baird. The second of these works exhibits a special direction of Cope's interest, namely the extremely varied structure of the paired copulatory organs of snakes, the hemipenes, which he figured for no less than 235 species in his *Classification of the Ophidia* (1895). The structure of the hemipenis, though subject to recurrent parallel or convergent evolution, and thus significant mainly at the generic level, has required the attention of herpetologists interested in the taxonomy of snakes ever since.

Cope's last service to American Natural History was as editor-in-chief of the *American Naturalist,* 1887–1897. This gave him a ready outlet for short notes and comments, as editorials and reviews. Osborn, his biographer, aptly compares him with Lamarck; Cope was indeed a "neo-Lamarckian," believing firmly in evolution, but equally in evolution through direct influence of the environment. His mind was brilliant and polemical rather than scholarly and constructive, or, for that matter, critical. It gave off ideas and published papers like a fountain; his bibliography lists no less than 1,395 titles. Allowing for all his carelessness

JOHN VAN DENBURGH



LEONHARD STEJNEGER



CHARLES L. CAMP

LAURENCE KLAUBER

and errors, Cope was the most stimulating figure in North American zoology in the last half of the nineteenth century.

Leonhard Stejneger (b. 1851, d. 1943) is the next great figure in American herpetology, contrasting as sharply with Cope as with Boulenger. He would have been mainly a contemporary of Cope's, had it not been that he came late to herpetology, at the age of thirty-eight, with a distinguished ornithological career behind him, and that Cope died at fifty-seven, whereas Stejneger lived to be ninety-one. The two herpetological careers overlapped for eight years, not without resounding clashes.

Leonhard Hess Stejneger was born in Bergen, Norway. He was educated in the schools at Bergen, by private tutor, and at the University of Kristiana. He first studied medicine, in order to take the courses in zoology and botany; when he found the prospect of a medical career not to his liking, he planned to go into the family business and he entered the school of law and graduated in 1875 as *cand. jur.* When the business failed, he determined to make a profession of zoology, instead of a hobby; and as there were few opportunities for positions in this field in Europe (let alone Norway), and on the advice of friends, he emigrated to the United States. This was in 1881; he went directly to the Smithsonian Institution, and seems at once to have been given temporary employment in the National Museum by Baird. His first eight years of work were in the field of ornithology, to which he contributed a notable series of reports and the excellent volume for birds in the Riverside Natural History. This period also included his field work, financed through the United States Signal Service, on the Commander Islands, and this left an indelible stamp on his interests, as may be seen from his ambitious and sound plan for the exploration of eastern Asia (1902), his effective contributions to the herpetology of China and Japan, his participation in the work of the Fur Seal Commission, and his life of Steller.

In 1889, on the resignation of H. C. Yarrow from the curatorship of herpetology at the National Museum, Stejneger was persuaded to take charge of this Division, and turned his attention thereafter almost exclusively to the systematics of amphibians and reptiles. He took an active part in the early field work of the United States Biological Survey in the western United States, made small collections in Japan in 1896 and 1897, and took part in a collecting expedition in Puerto Rico in 1900. Thereafter he devoted himself more and more to the description of the collections flowing into the National Museum from miscellaneous sources. He was made Head Curator of Biology in 1911. The Division of Herpetology is now in charge of Dr. Doris M. Cochran (1898–), who came as Aid in 1919.

Next to the *Herpetology of Japan* (1907), Stejneger's largest herpetological works were *The Poisonous Snakes of North America* (1895), *The Herpetology of Porto Rico* (1904), and a paper summarizing the Chinese collections in the National Museum. His smaller papers were devoted to the fauna of the United States, Mexico and Central America, the Philippines, and the West Indies, with a few from Africa and South America for good measure. His descriptions of new species are models of formal taxonomic work.

When Cope produced his volume on the crocodilians, lizards, and snakes of North America, the turtles had been reserved for a separate monographic report by the comparative anatomist Georg Baur (b. 1860, d. 1898). Baur came to the United States in 1884, and by the decade of 1890 had become the leading student of the morphology and evolution of the turtle group. He made a productive and stimulating expedition to the Galapagos Islands in 1891, and joined the staff of the University of Chicago in 1892. When Baur returned to Germany to die, Stejneger took over the project for a major work on the turtles of North America. As his time became absorbed in administrative duties, the turtle volume received only desultory attention; but he was never able to bring himself to give it up, and as result the great collection of these creatures at the United States National Museum was unavailable to other students for forty years. The monographic volume on turtles is still a desideratum.

Stejneger's scholarly and critical mind was disturbed by the looseness of description of species, the failure to designate type specimens and type localities, and the indifference to orderly rules of nomenclature exhibited, in quite contrasting ways, by both Boulenger and Cope. He introduced into descriptive herpetology the meticulous description of single specimens, which has proved to be disastrous for a usable taxonomy in the hands of some of his followers. Stejneger never explicitly recognized the "newer theory of taxonomy as a system of group concepts based on inferences about populations from samples."[10] The Boulengerian description of *the species* was a "paradigm" (to take over a grammatical term); and is implicit in Simpson's employment of the term "hypodigm"[11] for the sum of type material available to the describer or redescriber. Malcolm Smith comments on this problem in the first of his volumes of the *Fauna of British India.* The lesson from Stejneger of careful designation of type specimens and of type localities, the essence of his method, was an essential advance in descriptive technique.

The need for the establishment of uniform international rules of zoological nomenclature seems to have come into focus at the Fourth International Congress of Zoology, at Cambridge, England, in 1898. Stejneger attended this meeting on the occasion of his first return to Europe, which had carried him to his birthplace on museum business, and was elected a member of the first commission for nomenclature. He became increasingly involved in nomenclatural discussion and debate, and in the succeeding meetings of the Zoological Congresses.

The interest in nomenclature, and still more his treatment of its problems, seem to reflect something of the legal training of Stejneger's youth. The most constructive herpetological result of this interest was the *Check List of North American Amphibians and Reptiles*, in which Thomas Barbour joined as junior author. The five editions of this work, 1917 to 1943, witnessed a development of American herpetology and a multiplication of American herpetologists quite beyond prediction.

Leonhard Stejneger was the last herpetologist who can be thought of as dominating the field for a long generation. It is characteristic that the legion of his heirs should be so numerous, so much equals, and on the whole so cooperative. The remaining history of herpetology in North America is a history of the establishment of active herpetological work at a whole series of nationwide centers, sometimes with whole groups of active graduate students pursuing "problems."

---

10. George Gaylord Simpson, 1940, "Types in Modern Taxonomy," *Amer. Journ. Sci.*, 238:417.

11. *Ibid.*

Herpetology at University Museums

As a contemporary of Baird, and thus at the beginning of our century of herpetology, Louis Agassiz (b. 1807, d. 1873) appeared upon the New England scene and set in motion the greatest of university research museums, the Museum of Comparative Zoology at Harvard. Among Agassiz' varied interests, the turtles held high place; but this was equally, perhaps more, for their embryology than for their systematics. The prestige of Agassiz in America, as teacher and as exemplar of the "savant," was something America greatly needed. It had been only too easy to poke fun at the impractical and ridiculous, or even ludicrous, Rafinesque, and naturalists of sounder mind have been ridiculed by the practical; one may recall with shame the portrait of a naturalist set forth in the last of the Leatherstocking tales, *The Prairie.* Agassiz was no such naturalist—farmer and merchant and stagecoach driver, woman of fashion and bluestocking, college professor and schoolboy, all instantly fell under the spell of his greatness, which consisted, in fact, in his ability to convince them all of the greatness of natural history. An idea of the prestige of Agassiz at Cambridge in the eighteen-fifties is to be gained from the examination of the four volumes of his *Contributions to the Natural History of the United States of America,* with their superb lithographic illustration, and from the list of private subscribers who made possible the publication of so ambitious a work. The reader should not miss the bit of "inside dope" happily preserved by Dallas Lore Sharp in "Turtle eggs for Agassiz" (in *The Face of the Fields,* 1911).

Agassiz left a research museum as his greatest legacy to his adopted country, under the direction of his son Alexander, in many little known respects a greater man than his father. Louis Agassiz had himself accumulated great herpetological collections for the new Museum of Comparative Zoology—collections from the Amazon, for example—literally by the barrel. The zoologist who fell heir to these riches, Samuel Garman (b. 1843, d. 1927), after some notable contributions to the herpetology of North America, the West Indies, and the Galapagos, turned his attention more and more to studies of fishes. No full time herpetologist appeared at the "M. C. Z" until Thomas Barbour (b. 1884, d. 1946) took over the curatorship of the division in 1910, while still a graduate student at Harvard. He became director in 1927. His interest in foreign travel, and especially in animal geography, had been whetted by diligent boyhood reading of Wallace and Bates, Belt and Hudson. After a prolonged wedding trip through the East Indies in 1906, he devoted himself more and more to the West Indies and Panama. In the Canal Zone he was perhaps more than any other person responsible for the preservation of Barro Colorado Island as a natural laboratory—and as a living exhibit of the tropical forest made accessible to the biologists of the United States (and of the world)—either for a glimpse of its magnificent plants and animals, or for prolonged study. Barbour's large frame and booming voice, together with the prestige of his wealth and influence, made him a dominant figure wherever he appeared. It was necessary to know him more intimately to appreciate his generous and soft-hearted and often emotional side. Wealth could not save him from bitter and undeserved blows of fate. His herpetological work suffered from a readily forgivable overconfidence in his own powers. He literally worshiped Leonhard Stejneger, and joined him happily in the production of the successive editions of the *Check List.* His autobiographical *A Naturalist at Large* (1943) gives a vivid view of "T. B.'s" immensely interesting personality. Barbour placed the curatorship of the herpetological collection more and more in the hands of a young Englishman, Arthur Loveridge (b. 1891), already with long experience in Africa. Since 1924 the collections have benefited from Loveridge's competent field work in Africa and Australia. Loveridge's published work has caught up some of the accumulations of knowledge since the time of Boulenger's *Catalogues.*

While Curator of the Zoological Museum at the University of Michigan, Alexander G. Ruthven (b. 1882) had occupied himself with studies of local herpetology, and in 1906 had engaged on an active field expedition, with an essentially ecological outlook, in New Mexico, under the auspices of the American Museum. He then addressed himself to the revision of an American genus of snakes, *Thamnophis* (the garter snakes), the taxonomy of which had been left in hopeless confusion by Cope. Perhaps mainly encouraged by Stejneger, Ruthven undertook the study of what then seemed an enormous material, drawing upon Raymond Pearl for advice as to biometric method and, by 1908, producing a measure of order in what proved to be, by example, a work of the most crucial influence in subsequent herpetological studies in America. This was his *Variations and Genetic Relations of the Garter-Snakes* published as Bulletin 61 of the United States National Museum.

By limiting his field to a single well-defined genus, Ruthven set a pattern for further revisionary studies that lent themselves to a new mode in herpetology, the Ph.D. thesis. The University of Michigan itself, under Ruthven's directorship and rejuvenation of its museum program, became the leading center of herpetological training at the level of the university graduate school. Such university-fostered research is clearly the major herpetological phenomenon in America during the first half of the twentieth century. The succession of herpetologists in the University Museum at Ann Arbor was via Helen Thompson Gaige, long herpetological editor of the journal *Copeia,* to Norman Hartweg and Charles F. Walker, with the continuing association of L. C. Stuart. In another direction the Michigan School, derived directly from Ruthven's regime at the University Museum, leads to the scholarly Frank N. Blanchard (b. 1888, d. 1937) and to his aid and friend, Howard K. Gloyd (b. 1902) who subsequently became director of the Chicago Academy of Sciences, which thus developed as a center of herpetological studies and publication. William H. Stickel (b. 1912) of the United States Fish and Wildlife Service affords another example of the competent training of the students who came under Blanchard's influence.

During Ruthven's regime the reorganization of the University Museums (Paleontology, Botany, and Anthropology were combined with the Museum of Zoology) as a separate university department was realized, both in organization and in a separate new building. That the separation of the museum from the teaching departments associated with it is of vital importance is shown by the fate of departmental collections in colleges and universities the country over. That fate has been neglect, dispersal, sale, or total loss, as the heads of departments changed. Revitalized museum programs in universities, or the establishment of new ones, in more or less conscious imitation of the museum developments at Harvard and Michigan, have been almost a sign of the times, though some universities have continued to dispose of their collections, which have frequently gone to the large public museums. Notable herpetological centers at universities, with teachers and graduate students in this field, have flourished at Cornell, Rochester, California, Florida, Illinois, Iowa, Kansas, Louisville, Texas, Tulane, Colorado, Brigham Young, Utah, and the College of Puget Sound.

Among university museums maintaining expanding research collections, the high level of systematic studies at the Museum of Vertebrate Zoology at the University of California at Berkeley requires mention. Joseph C. Grinnell, the great first director, took part in studies on the amphibians and reptiles of California and furthered the work of Charles Lewis Camp (b. 1893) on the California fauna. Grinnell and Camp now have an able herpetological successor at Berkeley in Robert C. Stebbins, Jr., and with Raymond C. Cowles at the University of California at Los Angeles, Tracy Storer at the Agricultural College at Davis, and George S. Myers and a group of active students at Stanford University, California, has produced and is producing an active herpetological group, which has followed up the earlier work of van Denburgh, to be mentioned below.

Herpetology in American Public Museums

The larger public museums, with their dual organization as instruments of public education and institutes of research, continue to be the major centers of systematic herpetology. Such endowed museums are an especially American phenomenon, though notably represented in Europe by the Natur-Museum of the Senckenbergische Naturforschende Gesellschaft, at Frankfurt am Main. At the oldest of these in America, the museum of the Academy of Natural Sciences of Philadelphia, herpetology unfortunately failed to receive support after the death of Cope, whose herptological collections were left to the Academy. Arthur Erwin Brown (b. 1850, d. 1910), of the Zoological Society of Philadelphia, served usefully as interim aid. Emmett Reid Dunn (b. 1894), from near-by Haverford College, himself in some respects not unlike Cope in fertility of mind, has long served the Academy as honorary curator of herpetology; but the Cope Collection needed and deserved a full-time herpetologist as curator. The decline of herpetology at the Academy came during the period of most active expansion of the field in Washington and New York.

The importance of the United States National Museum to American herpetology has already been outlined. The American Museum of Natural History in New York City came late to an independent Division of Reptiles. Its first curator was Mary Cynthia Dickerson (b. 1866, d. 1923), whose reputation was made by her *Frog Book* (1906), with its competent photographic illustration by herself. The slenderness of her subsequent herpetological output must be understood in the light of her creation of the first significant museum magazine, the journal now known as *Natural History*. Her herpetological importance must be weighted also for her furtherance of the careers of a succession of young naturalists—Charles Lewis Camp, Emmett Reid Dunn, Gladwyn Kingsley Noble, and myself. Noble succeeded her as Curator of Herpetology, as I believe she had planned.

G. K. Noble (b. 1894, d. 1940) had been exposed equally to the influences of the Museum of Comparative Zoology and the laboratories of the Department of Zoology at Harvard and to the anatomical and phylogenetic school of William King Gregory at Columbia. He brought to the museum curatorship in New York the plan to graft laboratory methods on taxonomic procedure, and to expand the work of his division into other aspects of natural history than the purely systematic. With lavish financial support from trustees of the museum, he created a new department of "Biology"; but he could never bring himself to give up the curatorship of herpetology. His contribution to experimental biology lay in acquaintance with and use of novel experimental animals. His contribution to taxonomy consisted in the application of Nicholl's suggestions as to the classification of the frogs, with renewed anatomical and developmental studies. Animal behavior and animal psychology led him into studies on fishes, and to the application of ideas from bird-study to herpetology, especially to courtship in lizards (1933). His most important work, *The Biology of the Amphibia* (1931) well expresses the breadth of his interests. Noble's long succession of herpetological assistants (not to mention those in biology) began with myself and ended, at his sudden death, with Charles M. Bogert (b. 1908), with our jointly valued friend Clifford H. Pope (b. 1899) at about the middle of the series. Bogert has happily continued the tradition of a welding of experimental and anatomical techniques into a "new systematics."

The Carnegie Museum in Pittsburgh built up herpetological collections, beginning with the Haseman expeditions to South America (primarily for fishes), and has maintained a Division of Herpetology under the curatorship of M. Graham Netting (b. 1904) since 1925. At the Chicago Natural History Museum (then Field Museum) a Division of Reptiles was organized by myself in 1922. This has been under the curatorship of Clifford H. Pope (b. 1899) since 1941.

In the West the public museum as research institute is represented only by the museum of the California Academy of Sciences at San Francisco. This institution has had a distinguished herpetological program since the eighteen-nineties. The publishing career of Dr. John van Denburgh (b. 1872, d. 1924) extended from 1894 to 1924. He was effectively aided by Joseph R. Slevin in building up the collection, the domain of which was envisaged as the Pacific Ocean and its bordering lands. Notable in the history of the Academy was the definitive collecting in the zoologically classic archipelago of the Galapagos Islands. The Academy has also taken the lead in the exploration of the Lower California Peninsula (Baja California).

Several of the larger museums and various university museums of the United States have engaged in the exploration of Mexico and Central America, which naturally invite the interest of herpetologists. Building upon the works of Bocourt and Günther, our knowledge of Mexican herpetology in particular has been brought to the advanced state in which check lists of the fauna could be prepared. Check lists of the snakes (1945), amphibians (1948), and of the remaining reptiles (1950) by Hobart M. Smith and Edward H. Taylor summarize their own work and that of others.

The Canadian fauna of amphibians and reptiles being relatively impoverished, herpetology has been little more than an appendage to the active studies, on other groups of vertebrates, that have long flourished in Canada. Herpetological collections have nevertheless accumulated, especially at the Royal Ontario Museum with E. B. S. Logier, at the Provincial Museum of British Columbia under G. Clifford Carl. This fauna has been supplied with a check list by R. Colin Mills (1948).

Herpetology in Zoological Gardens

The relations of zoological gardens with the main currents of herpetological thought depend on the personalities involved. The reptile house, at every zoo, it is said, is next only to the monkey house in popular interest. Thus a curator of reptiles is a necessity for every zoo staff, and these are usually drawn from the host of amateur snake-keepers, who, in America, replace the lizard-lovers of Europe. Thus it is natural that the herpetologist at a zoo should find himself involved in popular writing and, vice versa, the zoo job has an attraction for the snake-keeper with a flair for newspaper writing; these relations are exemplified in the career of Raymond Lee Ditmars (b. 1876, d. 1942) long curator of reptiles at the Bronx Zoo of the New York Zoological Society. For twenty or more years Ditmars' books were as books of the Bible to aspiring young herpetologists in the United States, to the dismay of those of us who saw their grave defects—that they treated herpetological knowledge as a closed book, instead of as the mere beginning of knowledge; that they made it seem that herpetology began with Ditmars; and that they encouraged the idea that the whole duty of a herpetologist lies in repeating a modicum of knowledge as a kind of patter, on all possible occasions. In these respects Ditmars' *The Reptile Book* (1907) fell far short of Miss Dickerson's *Frog Book*. The appearance of more serious handbooks for the young, and especially of handbooks that suggest things to do and things to observe, now definitely relegates the Ditmars era to the past. These newer books may be listed in order. For the United States, at least, it is to be hoped that they will stimulate a new period of herpetological investigation, in new and varied directions, as did the *Erpétologie générale* a hundred years before.

1933. *Handbook of Frogs* (3rd ed., 1949), by A. H. and A. A. Wright.
1937. *Snakes Alive and How They Live*, by Clifford H. Pope.
1939. *The Turtles of North America*, by Clifford H. Pope.
1941. *Field Book of Snakes*, by Karl P. Schmidt and D. Dwight Davis.
1943. *Handbook of Salamanders*, by Sherman C. Bishop.
1946. *Handbook of Lizards*, by Hobart M. Smith.
1952. *Handbook of Turtles*, by Archie F. Carr.

Ditmars' position in New York has been filled by a member of the new American school of professionally trained herpetologists, J. A. Oliver (b. 1914), lately of the American Museum and the University of Florida.

As the London Zoo brought the much too sessile Boulenger into contact with living amphibians and reptiles, the great zoo at Berlin, though never with a professional herpetologist as curator, was a source of the fine photographic illustration of Brehm's *Tierleben*. The Cairo Zoological Gardens were long in charge of Major S. S. Flower, whose lifelong herpetological interests continued after his retirement to England.

American zoos have been fortunate in their strong herpetological sections. Roger Conant carried much of the influence of the Michigan school from Toledo to Philadelphia, where he continued the precedent of scientific studies set by A. E. Brown. In San Diego C. B. Perkins and C. E. Shaw have made excellent use in the favorable climate of Perkins' design of a reptile house, which is quite as effective in San Diego as is the museum-type building, designed by Miss Procter, in London and Washington.

An American phenomenon, the so-called "Snake Farm," has grown up in response to the great interest in snakes on the part of the general public. This is to no small degree a modern counterpart of the performances of the North African and Oriental snake-charmers. It might be passed over without mention here were it not that the Florida Reptile Institute, under the able showman E. Ross Allen, has developed *via* a business of herpetological supply into ambitious herpetological research. In the serpentaria of the institutes manufacturing antivenin as a remedy for snake bite, the collections of living snakes yield a by-product in the form of snake shows that correspond exactly in an inverted relation to those of the snake farm, as in São Paulo, Brazil, Bangkok, Siam, or Port Elizabeth, South Africa.

The Amateur in Herpetology

Natural history has always been open to amateurs and self-education in this field has often preceded book knowledge. The positions in public and university museums are so few that the few actual professionals in herpetology have always welcomed the aid of volunteer students. The enthusiastic amateur needs only to follow the Huxleyan motto *tenax propositi* to be able to vie with professionals at their own level. It is for the amateur and beginner that the general popular books are written. Catherine C. Hopley's *Snakes: Curiosities and Wonders of Serpent Life* (1882), written, curiously enough, by an Englishwoman caught in South Carolina by the Civil War, helped to set the pattern for Mary Cynthia Dickerson and Raymond Lee Ditmars.

At the more serious level, it may be remembered that the only education in zoology available a century ago lay in the preparation for a medical career. Thus medical men were long the principal leaders in herpetology as in natural history in general. One may wish that the avocation of natural history studies had persisted as a custom among medical men, to whom studies in the field would combine recreation with the promotion of science, and to whom comparative anatomy would be a readily opened book. A late exemplar of the happy combination of a medical career with a life-long interest in herpetology was the distinguished and remarkable Howard A. Kelly (b. 1858, d. 1943), Professor of Gynecology at Johns Hopkins University. Among our colleagues of 1950 it is refugees with a European medical training that take up functional comparative anatomy. My two American correspondents who pursue both herpetology as such and the practice of medicine are Dr. Murray L. Johnson of Tacoma, Washington, and Dr. Frederick A. Shannon, of Wickenburg, Arizona.

The amateur who reaches the highest professional standards is likely to bring a fertilizing element of originality to his work. The most conspicuous illustration of the herpetological amateur turned professional in America is the career of Dr. Laurence M. Klauber (b. 1883). Beginning with desultory collecting of living snakes and lizards for the San Diego Zoo, he was led first to systematize his observations during automobile travel at night. As night collecting proved to be vastly productive, often of species previously regarded as rare, Klauber began to build a great personal collection; as this grew, he pioneered in methods of statistical study of variation in snakes, a natural turn of interest on account of his mathematical training as an engineer. In the last decade of our history he was at work on a monographic account of that most distinctive of American snakes, the rattlesnake. His contribution to systematics in the fauna of the American Southwest consists in reviewing genus after genus in terms so much more exact than in any earlier work as to be beyond comparison. These studies have supplied secure foundations for further studies in any direction, which is a major function of taxonomic zoology.

Regional Schools of Herpetology

With the Boulengerian *Catalogues* available, independent schools of herpetology could grow up in South Africa, Australia, and South America. In the Union of South Africa the existence of a great number of regional museums greatly furthered the independent growth of herpetology focused on the rich fauna of the region. At the Albany Museum in Grahamstown, John Hewitt's papers begin in 1909, and two books by Walter Rose of Cape Town, *Veldt and Vlei* (1929) and *The Reptiles and Amphibians of Southern Africa* (1950), afford an introduction to this fauna at the popular level. Among numerous able students, Vivian F. FitzSimons (b. 1901), at the Transvaal Museum, took the lead with his volume on *The Lizards of South Africa* (1943). *A Guide to the Snakes of Uganda* (1938), by Captain Charles R. S. Pitman, with excellent colored plates, ingeniously financed by subscription, represents still another competent work by an amateur.

In Australia an independent center of herpetology grew up at the Australian Museum in Sydney under J. R. Kinghorn. The existence of the museums of the several states in Australia has furthered publication and popularization, as in South Africa.

In South America, herpetology has flourished mainly in the Argentine at Buenos Aires and in Brazil at Rio de Janeiro and São Paulo, with immigrant scholars from Europe, and with European and North American trained native students. Miguel and Kati Fernandez, in the Argentine, have produced an excellent account of life histories of frogs, and Bertha Lutz, drawing upon her own and her father's notes, has taken the step from taxonomy to ecology at Rio. The work of Afranio do Amaral, long director at the Instituto Butantan, has been mainly on lizards and snakes. The extraordinary life history of Darwin's frog, in which the tadpoles are brought to maturity in the vocal sac of the male, was worked out by Karl Pflaumer in Chile between 1926 and 1930 ("Beobachtungen an Rhinoderma darwinii," *Zool. Garten* [1934], n.s., 7:131–134). The Brazilian group of herpetologists is especially strong at the half-century mark in 1950.

The Philippine fauna, after the acquisition of the islands by the United States in 1898, became tributary to the United States National Museum, and was further exploited herpetologically by the active collecting and publication of E. H. Taylor —quite in the pattern of the European colonies, but with the summary volumes published by the Philippine Bureau of Science.

The independence of Chinese herpetology from European and American centers was forecast before the drawing of the "Bamboo Curtain" by the work of C. C. Liu, beginning in 1930 and culminating in his large work on *The Amphibians of West China* (1950). Dr. Liu had the advantage of close relations with his American herpetological colleagues, and could build on the work of his teacher Dr. Alice M. Boring (b. 1883) and on the contributions to the herpetology of China of Clifford H. Pope.

Herpetological Societies and Journals

The growth of the herpetological societies that maintain journals as outlet for publication had a most important influence on the rise of herpetology in America in the twentieth century. *Copeia,* now the journal of the American Society of Ichthyologists and Herpetologists, begun in 1913, was at first edited and privately published by John T. Nichols, of The American Museum of Natural History. Its function as envisaged by him was to serve as an outlet for short papers on miscellaneous minor observations of all sorts on cold-blooded vertebrates. The journal was taken over by the Society in 1924 under the editorship of E. R. Dunn, and was expanded and reorganized to publish longer and more important papers in 1930, under the editorship of Helen Thompson Gaige. I served as herpetological editor from 1937 to 1950, followed by Norman Hartweg. The miscellaneous note section continues the tradition of minor notes, often by beginners in the field, and thus has served as an effective training school for the writing of papers. Research is fostered by grants-in-aid from the Society's funds.

Like *Copeia,* the journal *Herpetologica* was at first privately published by Major Chapman Grant, of San Diego; it was founded in 1936, and was edited by Major Grant and Walter L. Necker until 1943, subsequently by Major Grant alone. The Herpetologists' League was oganized in 1946 in order to strengthen support for *Herpetologica.*

It is gratifying to note the birth of the *British Journal of Herpetology,* in 1948, as the organ of the newly organized British Herpetological Society.

The influence of both societies and journals has plainly been to expand the numbers of herpetologists, to fire more and more amateurs with the ambition to publish their studies and observations, and to direct an increasing number of students into university training.

Anatomy[12]

Interest in the anatomy of amphibians and reptiles was split three ways during the century under discussion. Simple description of the anatomy of animals (and plants) has always been one of the main duties of morphologists, and this elementary recording of facts continued throughout the century. The taxonomy of the higher categories is based almost entirely on morphological differences and similarities, and the pursuit of taxonomic interests added greatly to our knowledge of the anatomy of amphibians and reptiles. Far more important than either of these was the enormous stimulus to anatomical research that came from the publication of the *Origin of Species.* Amphibians and reptiles occupy a strategic position between the fishes and the mammals, and were closely studied in the intensive search for the phylogeny of vertebrate structures.

In 1850 the field of vertebrate anatomy was still dominated by the methods and ideas of Cuvier in France, Meckel and Johannes Müller in Germany, and Owen in England. The works of these four and their contemporaries, aside from their philosophical content, laid the foundation for modern descriptions of the anatomy of vertebrates. Straight description of structure, perhaps because it usually does not attempt to evaluate data and therefore demands little background, is available doctor's thesis material. Many of the hundreds of anatomical

12. Contributed by my colleague, D. Dwight Davis, Curator of Anatomy, Chicago Natural History Museum.

papers published during the past century are by obscure persons who are never heard of again, or by men who later became noted in nonmorphological fields. A few, however, stand out because of the number or importance of their studies. Owen himself carried over into the post-1850 period. The first volume of his *Anatomy of Vertebrates,* which covers amphibians and reptiles, appeared in 1866 when Owen was sixty-two years old. St. George Mivart (b. 1827, d. 1900), an isolated half-mystical figure who for many years was Lecturer in Comparative Anatomy at St. Mary's Hospital in London, contributed several careful descriptions of the skeleton and muscles of amphibians and lizards before he turned his attention exclusively to mammals. William Kitchen Parker (b. 1823, d. 1890) was a British physician with a passionate love of nature that expressed itself in a series of meticulous monographs, illustrated with plates drawn by himself, on the structure and development of the skull and pectoral girdle of various amphibians and reptiles. Parker was greatly handicapped by the fact that he could not read German.

That remarkable Swede, Gustaf Retzius (b. 1842, d. 1919), could hardly have failed to contribute to our knowledge of the morphology of amphibians and reptiles. Retzius was the son of the distinguished anatomist and anthropologist, Anders Adolf Retzius, who in turn was the son of a distinguished natural scientist. Retzius was a friend of the great German anatomist, Johannes Müller. His work was almost wholly descriptive, painstakingly detailed, and illustrated largely by himself. The tremendous *Das Gehörorgan der Wirbelthiere* (2 vols., 1881–1884) contains meticulous descriptions of the auditory apparatus of many amphibians and reptiles. Later, after he had turned his attention to the structure of sex cells, he described the spermatozoa of many amphibians and reptiles.

The outstanding descriptive work of this era is *Die Anatomie des Frosches,* which was addressed to physiologists rather than anatomists. The first edition of this famous work, by Alexander Ecker (b. 1816, d. 1887) and Robert Wiedersheim (b. 1848, d. 1923), appeared in three parts between 1864 and 1882. Both Ecker and Wiedersheim were at the University of Freiburg, where Ecker was Professor of Human and Comparative Anatomy and Wiedersheim Extraordinary Professor. A second edition, completely rewritten by Ernst Gaupp (b. 1865, d. 1916), also of Freiburg, appeared in three parts between 1896 and 1904. An English edition of the first German edition, translated by George Haslam, was published in London in 1889. Other frog anatomies during this era were by Mivart (1874) and A. M. Marshall (1882) in England, and by S. J. Holmes (1916) in America. It is extraordinary that a comparable work on a salamander did not appear until 1934, when *The Anatomy of the Salamander* [*Salamander maculosa*], by Eric T. B. Francis, was published in England. Still more remarkable is the fact that no modern descriptive anatomy of any reptile has ever appeared.

The most ambitious compendium of accumulated data on the morphology of amphibians and reptiles appeared in Bronn's *Klassen und Ordnungen des Thierreichs.* The herpetological volumes, running to more than 2,800 pages and 223 lithographed plates, were published between 1873 and 1890. They were compiled by Christian Karl Hoffmann (b. 1841, d. 1903) of the University of Leiden. Although now sadly out of date, Hoffmann's is still the only general compilation of anatomical data for amphibians and reptiles.

The classical treatise on the embryology of an amphibian is Goette's folio

Die Entwicklungsgeschichte der Unke (Bombinator igneus) als Grundlage einer vergleichenden Morphologie der Wirbelthiere (1875). Alexander Goette (b. 1840, d. 1922) was greatly influenced by the embryologist von Baer, and was himself a teacher of Wilhelm Roux. His *Bombinator* monograph was the basis for his purely mechanistic theory of evolution, which undoubtedly influenced Roux's later mechanistic concept of morphogenesis. It is also the prototype of all later descriptive work on frog embryology.

The second half of the nineteenth century was the Golden Age of the morphological sciences. Knowledge of the structure and development of amphibians and reptiles, along with the other vertebrates, was enormously extended and deepened during this period. Carl Gegenbaur (b. 1826, d. 1903), more than any other man, is identified with this flowering of morphological interest. Darwin's evolutionary ideas were becoming current at the very beginning of Gegenbaur's career, and he grasped their significance at once, realizing that the phylogeny of vertebrate structure provided comparative anatomy with the conceptual framework that had previously been lacking. Our knowledge and understanding of the structure of amphibians and reptiles was enormously increased as a by-product of the research resulting from this reorientation.

Gegenbaur himself contributed directly in a number of publications, but his indirect influence on herpetology was far more important. Among his assistants during his long career at Jena (1855–1872) and Heidelberg (1872–1900), Max Fürbringer, Friedrich Maurer, Ernst Göppert, and Georg Ruge added greatly to the fund of knowledge, especially of the musculature and its innervation. His pupils carried Gegenbaur's ideas beyond Jena and Heidelberg, and even beyond the borders of Germany. Although the Gegenbaur tradition was never strong in England or America, his pupils Hans Gadow (b. 1855, d. 1927) in England and H. H. Wilder (b. 1864, d. 1928) and W. B. Scott (b. 1858, d. 1947) in America were active and influential in the English-speaking world.

Schools of associated workers, often with special orientations and traditions that ran through several generations, were characteristic of central Europe. These begin with one vigorous personality, who infects and often dominates others. The Gegenbaur school, with its unflagging pursuit of the phylogeny of structures via interpretative homologies, has already been mentioned. The output of this school ran heavily to myology, a subject in which Gegenbauer himself was little interested. The myological orientation is probably attributable to Max Fürbringer (b. 1846, d. 1920).

The Freiburg school, beginning with Ecker and *Die Anatomie des Frosches,* and continuing through Gaupp and Wiedersheim, centered its attention largely on amphibians. In Vienna the towering figure of Joseph Hyrtl (b. 1811, d. 1894) began a dynasty that lasted through three generations, until it was destroyed by the Nazis in the years before World War II. Hyrtl's interest in the vascular system is strongly reflected in the work of Emil Zuckerkandl (b. 1849, d. 1910), Julius Tandler (b. 1869, d. 1936), and Anton Hafferl, and in the painstaking solution of problems arising in the medical dissecting room, which repeatedly inspired extensive comparative researches based on the museum collections, and is evident in most of the Vienna studies of this era. Most of this work, which has a characteristic stamp, appeared in the *Denkschriften* and *Sitzungsberichte* of the Vienna Academy.

Outside Europe the outstanding example of a special anatomical "school" is probably the extensive work in South Africa, by various authors, on the cranial anatomy of amphibians studied by means of serial sections. This work, which falls in the second quarter of the twentieth century, is traceable to C. G. S. de Villiers, who was a student of Arnold Lang in Zürich.

The third great drive of morphological research is to provide a basis for taxonomy. This, of course, involves studying many representatives of a group—often every available genus. Two quite different goals are involved. One is to distinguish the groupings into which species, genera, or families may be partitioned; this is essentially analytical. The other is to determine the interrelationships among these groupings; this is essentially synthetic.

Although he was not an anatomist, G. A. Boulenger is chiefly responsible for the breakdown into families among the Reptilia that is in use today. Boulenger, in turn, drew heavily on Friedrich Hermann Stannius (b. 1808, d. 1883), a German comparative anatomist who, after studying under Johannes Müller, was professor at Rostock. The second edition of Stannius' *Handbuch der Anatomie der Wirbelthiere* (1854), which is set up in a taxonomic rather than an organ-system framework as the first (1846) edition was, is repeatedly cited by Boulenger.

Cope is Boulenger's counterpart for the Amphibia, and the modern arrangement of families of salamanders and frogs is essentially that of Cope, sharpened and refined by a host of later workers. H. H. Wilder made the important discovery of lunglessness in certain salamanders in 1894. G. E. Nicholls, who was Professor of Biology at Agra College, Agra, India, discovered the importance of the vertebral column in classifying Salientia (1916). And G. K. Noble drew the soft anatomy, especially the thigh musculature, into a general review of the classification of these animals (1923). Noble's work is further important for its emphasis on interrelationships rather than mere partitioning.

Edoardo Zavattari, of the Zoological Museum of the University of Turin, published in 1910–1911 a 122-page monograph on the hyoid muscles of lizards, describing and illustrating the patterns in a wide selection of species. This, plus earlier analytical work on the skeleton by Cope and others, and on the body and limb muscles by Fübringer, Gadow, and Maurer, formed the basis for a general review of the classification and interrelationships of the lizards by C. L. Camp (1923).

The foundation of the modern classification of turtles was laid by Boulenger. This was refined chiefly by the voluminous work of Georg Baur and Friedrich Siebenrock, both of whom were active but not very imaginative anatomists. Boulenger was also responsible for the framework of the modern classification of snakes. Boulenger's classification has been improved and corrected by many later workers. A brief review of the comparative anatomy of snakes and its implications was published as recently as 1951 by Bellairs and Underwood in *Biological Reviews*.

The outstanding student of the eye of reptiles was Gordon Lynn Walls (b. 1905), who built on the earlier work of the German, Victor Franz. Walls, formerly at Wayne University at Detroit and now at the University of California, emphasized the profound differences between the eyes of snakes and lizards, and made this the basis for his theory of the origin of snakes from noctural lizards. He described, among other things, the existence of physiologically yellow lenses that function as color filters for increasing visual acuity. All of Walls's work reflects a lively interest in functional mechanisms rather than static structure. His major work is *The Vertebrate Eye and Its Adaptive Radiation,* published by the Cranbrook Institute of Science in 1942.

Comparative functional anatomy, in which the description of adaptive mechanisms drives the student from the dissecting table to the living animal in the field and from the field or zoo to the dissecting table, is a relatively new direction of interest in verteberate anatomy. The phylogeny of adaptation may be pursued (as by Walls) and an understanding of the structures involved is often to be gained by the comparison of analogous, as distinguished from homologous, mechanisms. An outstanding representative of this fertile movement in herpetology was Walter Mosauer, a student of Franz Werner's in Vienna, who had made a notable contribution to the anatomy of snakes and to the understanding of their locomotor musculature before his untimely death in 1937. Mosauer had become a citizen of the United States and had taken his doctor's degree at the University of Michigan.

The Study of Snake Venom

The study of snake venoms forms a large chapter of herpetology. The scientific study of venoms and of the treatment of snakebite falls almost entirely within the period 1850–1950.

An important preliminary study by Dr. S. Weir Mitchell (b. 1829, d. 1914), in 1861, set the investigation of venoms and of the medical treatment of the bites of poisonous snakes on a critical and experimental basis. Sir Joseph Fayrer's *Thanatophidia of India* (1872) was supplemented by a series of papers on the physiological effects of the venoms of Indian snakes by Fayrer and Brunton (1872–1875), and further work was reported by A. J. Wall in *Indian Snake Poisons; Their Nature and Effects* (1883). The whole subject is then summarized by Mitchell and Reichert in *Researches upon the Venoms of Poisonous Serpents* (1886), in the Smithsonian Contributions to Knowledge.

A burst of interest in the treatment of snakebite came with the discovery that antivenins are produced in the blood of animals inoculated with small successive doses of venom, and that the degree of immunity can be built up by successively increasing the dosage of venom. The pioneer students were H. Sewall, working with rattlesnake venom and pigeons (1887), and Maurice Kaufmann, using the venom of the European viper and the guinea pig (1889). This discovery led directly to experiments by Marie Phisalix and G. Bertrand at the Paris Museum and A. Calmette at the Pasteur Institute at Lille on the use of the blood serum of immunized animals as an antidote in snake poisoning. This set the stage for the development of institutes for the production and distribution of antivenins for general use. Pasteur Institutes were established at Calcutta and Bangkok. The Instituto Butantan at São Paulo, Brazil, was set up as much for research as for antivenin production. The Mulford Drug Company's antivenin division in the United States (with its successors) grew out of the interest aroused by the Antivenin Institute of America, which published a *Bulletin* (1927–1932). In South Africa, centers of antivenin production were developed, as at Port Elizabeth. In Australia critical studies of snake venoms have been in progress under the direction of H. C. Kellaway since 1929. The enthusiastic interest aroused by the all-but-miraculous recoveries from serious cases of snake-poisoning in human beings after the injection of antivenin, together with the sound basis of fact as to immunization in general, led to great public interest and government support for such institutes.

The first major difficulty to develop in the treatment of snakebite with antivenin lies in the radical difference between the neurotoxic venoms of the cobra and its relatives and the haemotoxic venoms of the vipers and pit-vipers. This is especially complicated by the fact that the widespread South American rattlesnake, alone among the pit-vipers, has a powerfully neurotoxic venom. Furthermore, it soon developed that the antivenins were in general strictly specific. The fact that the venoms of the many different species of poisonous snakes are sharply peculiar to the species, and that the antivenin prepared from inoculation with venom of the banded rattlesnake, for example, would not serve as an antidote for the bite of the copperhead, led to the production of "polyvalent antivenins." The specificity of venoms may be sharply marked even within otherwise barely distinguishable races of a single species, and thus adds an example of the biochemical nature of species differentiation.

The antivenin institutes, in retrospect, appear to have acquired a "vested interest" in snake bite, and their statistics are in urgent need of critical review. In 1927, Dr. Dudley Jackson, of San Antonio, Texas, found that in rattlesnake bite, incisions and suction on the swollen limb would lead to a high percentage of cures *without* antivenin. Afranio do Amaral, long Director of the Instituto Butantan, was led to propose progressively greater dosages of antivenin, finally to the amount of 225 cc. This, on the face of it, introduces new dangers and new problems. At midcentury the subject is thus in need of a renewed objective and critical study.

Experimental Physiology and Embryology

The broad fields of experimental investigation into physiologic and developmental processes have had so great a growth in the 1850–1950 century, and their focus has been so much on the process and on the principles involved and so little on the particular experimental animal, that the history of the herpetological aspects of these sciences and their bearing on the growth of herpetology as a whole need not be elaborated here. A late bibliography of experimental embryology is available in Rugh's work with this title (1948). Salamanders, with their capacity for complete regeneration of limbs, have been especially favorable material for studies in regeneration (T. H. Morgan, *Regeneration*, 1901; E. Korschelt, *Regeneration and Transplantation*, 1907). For a conspectus of the literature on general physiology as applied to amphibians and reptiles reference may be made to Heilbrunn's *Outline of General Physiology* (1943) and to *Comparative Animal Physiology*, edited by C. Ladd Prosser (1950). The physiology of the whole animal, which relates it to its environment, is a part of ecology.

Ecology and Herpetology

Ecology, as natural history made critical and exact, stands in direct relation to modern herpetology, and requires thoughtful assessment of its origins and present status in this relation. Taxonomic herpetology in the Boulengerian Era remained consciously aloof from consideration of habitats, and geographic distribution was cited as if it were a matter of occurrence in space independent even of altitude. The characteristics that distinguish species were referred to as "useful" if they were useful to the taxonomist in his discrimination of systematic groups.

The realization that species and subspecies had to be revalued and redescribed in terms of the general environments and special habitat niches in which they occur came first from the side of popular natural history (e.g., Brehm's *Tierleben*). Laboratory studies of the reactions and tolerances of animals afford another of the roots of animal ecology. A pioneer paper in the United States was based by Alexander G. Ruthven on field studies in the American Southwest in 1906 (Ruthven, 1907), in which he was obviously influenced by C. C. Adams. Since that date there has been increasing interest in the observation of the biotic and physical environments in which amphibians and reptiles live, how they meet the adverse factors in their surroundings, and, in general, how they "behave" in relation to them. The importance of environmental observation to a definitive taxonomy is especially illustrated by the work of Henry S. Fitch on the garter snakes of the Pacific region (1940). Ecological observation, of course, stands on its own feet independent of its significance to taxonomy, and becomes increasingly independent as the taxonomy becomes mature, and thus a sound foundation for ecology. Ecology involves a vast variety of subsciences from physiography, meteorology, and chemistry to the complex of biotic relations, and more particularly for herpetology, the relation of animal life to its plant matrix. Finally, since animal behavior rests on the interaction of internal physiology and stimulus from the environment, the ecology of animals must particularly include their behavior, the study of which tends to be distinguished as the separate science of animal behavior. Physiological investigation in herpetological ecology is to be discerned in the continuing studies of Raymond B. Cowles (b. 1896) and of his student and colleague, C. M. Bogert, on the temperatures of amphibians and reptiles in relation to the temperature range of their environment. The sharpness of limitation to specific habitat niches reflects the long evolution of the reptile group; it is illustrated by the rock-crevice habitat of such lizards as *Sauromalus* in the American Southwest, and especially by *Xantusia henshawi* and *arizonae,* which live under the loose exfoliating rockflakes of rounded granite boulders. Courtship behavior, with the frequent correlation of the spacing of individual animals of breeding groups into territories, is an important field of study pioneered in herpetology by G. K. Noble (Noble and Bradley, 1933). The subject of "Home Ranges and Wanderings of Snakes" (*Copeia,* 1947, pp. 127–136) is summarized by William F. Stickel and James B. Cope. That the populations of amphibians and reptiles are often vast has long been known from their breeding aggregations. Actual measurements of population density are extraordinarily few. Pioneering studies in this direction rest on the techniques of marking individuals by tagging, toe-clipping, scale-clipping, or tattooing, pioneered by F. N. Blanchard in 1933. Cagle's paper in 1950, "The Life History of the Slider Turtle, *Pseudemys scripta troostii* (Holbrook)" in *Ecological Monographs* (20:31–54, 18 figs.) summarizes ten years of work in this field. The study of distribution depends directly on examination of the present environment and on speculations regarding the past changes in environment, i.e., on ecology and paleoecology. Studies on defensive and warning behavior involve the assessment of the function of venoms, especially in relation to mimicry and coloration. Sense perception and orientation have been studied in relation to food capture and to such phenomena as the movement of hatching seaturtles to water. The problem of isolating mechanisms between species (voice in frogs, for example) involves restudy of the so-called taxonomic characters in order to find out what they mean. Especially significant studies on the physiological isolation of the species of frogs and of populations of a single species have been made by John A. Moore (b. 1927) of Barnard College.

An ecological framework for studies of animal distribution was outlined by Richard Hesse in 1924 (*Tiergeographie auf oekologischer Grundlage,* Amer. ed. 1951). A framework by means of which past and future studies on the ecology of reptiles and amphibians can be brought into relation and correlation with other studies is provided by C. W. Allee, *et al., Principles of Animal Ecology* (1949).

At the midcentury the study of amphibians and reptiles may be seen to be in need of a world synthesis, perhaps a more elaborate one than that of the catalogues of the British Museum two generations earlier, but still essentially a systematic review. A review of the existing systematics of these groups should serve as a springboard from which the *new systematics* can be explored and applied, involving the reassessment of the classification from class to subspecies and population in the light of the advances in biology as a whole. The review envisaged would then be the basis also of a *new natural history,* in which studies of life histories and habits and behavior are brought into relation with comparative functional anatomy. The new systematics and the new anatomy are essential to the interpretation of the still growing body of knowledge of the extinct forms of both amphibians and reptiles. We thus envisage a major contribution from herpetology to an understanding of the evolution of the animal kingdom, with its vast perspective in time and its broad ramifications in the present.

BIBLIOGRAPHY

AGASSIZ, ELIZABETH CARY

1886. Louis Agassiz, His Life and Correspondence. 2 vols., illus. Boston: Houghton, Mifflin Co.

ANONYMOUS

1870. Duméril (André-Marie Constant). Grand Larousse, 6:1379.

1874. Peters (Guillaume-Charles Hartwig). Grand Larousse, 12:703–704.

1931. Miss Joan Proctor. The London Times, Sept. 21, 1931.

1941. G. K. Noble. Copeia, vol. for 1940, pp. 274–275, portr.

1951. Sherman C. Bishop, 1887–1951. Proc. Rochester Acad. Sci., Vol. 6 [portr. and text inserted without pagination before p. 327].

BARBOUR, THOMAS

1919. Boulenger, the man and his work. Nat. Hist., 19:566–567, portr.

1943. Naturalist at Large. xii + 314 pp., illus. Boston: Little, Brown and Co.

BARDELEBEN, KARL

1894. Joseph Hyrtl. Anat. Anz., 9:773–776.

BERTIN, LÉON

1939. Catalogue des types de poissons du Muséum National d'Histoire Naturelle. 1re pte. Cyclostomes et Selaciens. Bull. Mus. Natl. Hist., Nat., sér. 2, 11:51–98 [Historique des collections ichthyologiques du Museum, pp. 51–63].

B[lanford], W. T.

1900. John Anderson, M.D., LL.D., F.R.S. . . . , *Nature*, 62:529–531.

Bluntschli, Hans

1922. Max Fürbringer. Anat. Anz., 55:244–255, portr.

Boulenger, G. A.

1906. Reptiles and Batrachians, *in* The History of the collections . . . of the British Museum, vol. 2, pp. 517–531. London. British Museum.

1921. Liste des publications ichthyologiques et herpétologiques (1877–1920). Ann. Soc. Roy. Zool. Malac. Belgique, 52:11–88.

Cattell, Jaques, Ed.

1949. American Men of Science a Biographical Dictionary. 8th ed. [iv] + 2836 pp. Lancaster: The Science Press.

Dall, William Healey

1915. Spencer Fullerton Baird, a Biography including Selections from His Correspondence with Audubon, Agassiz, Dana, and Others. xvi + 462 pp., illus. Philadelphia: J. B. Lippincott Co.

Duméril, A. M. C.

1854. Notice sur G. Bibron. In Erpét. Gén., Vol. 7 [inserted 4 pp. notice after preface, unpaged].

Fischer, Albert Kenrick

1943. Leonhard Stejneger. Copeia, vol. for 1943, pp. 137–141.

Freytag, Günther E.

1948. Willy Wolterstorff. Ein Forscherleben für das Museum für Naturkunde und Vorgeschichte zu Magdeburg. Abh. Ber. Mus. Naturk. Magdeburg, 8:7–18, 1 pl.

Gloyd, Howard K.

1940. Frank Nelson Blanchard, Scholar and Teacher. *Herpetologica*, 1:197–208, illus.

Godman, Frederick Ducane

1915. Biologia Centrali-Americana Zoology, Botany and Archaeology. Introductory Volume, VIII + 149 pp., 2 pls., 8 maps. Privately published.

Gregory, William K.

1942. Gladwyn Kingsley Noble (1894–1940). Yearbook Amer. Philos. Soc., vol. for 1941, pp. 393–397.

Günther, A. C. L. G.

1886. Reptiles, History and Literature. Encyclopedia Britannica, ed. 9, 20:432–441.

Günther, A. C. L. G., and A. S. Woodward

1911. History of Herpetology. Encyclopedia Britannica, ed. 11, 23:136–141.

Günther, R. T.

1930. Bibliography of the works of Dr. Albert Günther. Ann. Mag. Nat. Hist., ser. 10, 6:233–286.

Haas, [Fritz]

1910. Professor Dr. O. Boettger†. Ent. Blatt., 6:267–268, portr.

Hay, O. P.

1898. George Baur. Science, n.s., 8:68–71.

Hertwig, Oscar

1905. Ann. Rep. Smithson. Inst. for 1904, pp. 787–791, portr.

MOSAUER, WALTER

1940. Franz Werner, 1867–1939. Herpétologica, 1:178–183, portr.

NORDENSKIÖLD, ERIK

1942. The History of Biology. xii + 629 [xv] pp. New York: Tudor Publishing Co.

N[ORMAN], J. R.

1938. Dr. G. A. Boulenger, F.R.S., Nature, 141:16–17.

OSBORN, HENRY FAIRFIELD

1931. Cope: Master Naturalist. The Life and Letters of Edward Cope, with a Bibliography of His Writings Classified by Subject. A Study of the Pioneer and Foundation Periods of Vertebrate Paleontology in America. xvi + 749 pp., illus. Princeton: Princeton Univ. Press.

PIETSCHMANN, V.

1919. Franz Steindachner. Ann. Naturhist. Mus. Wien, 33:47–48.

ROULE, LOUIS

1917. Notice nécrologique sur M. le Dr. Françoic Mocquard. Bull. Mus. Natl. Hist. Nat., 23:315–317.

RUTHVEN, ALEXANDER G.

1931. A Naturalist in a University Museum. 143 pp., illus. Ann Arbor: Privately printed.

1936. Helen Thompson Gaige. Herpetologica, 1:1–2, portr.

SCHMIDT, KARL P.

1936. Robert Kennicott, Founder of Museums. Program of Activities, Chicago Acad. Sci., 7:3–8.

1937. Frank Nelson Blanchard, 1888–1937. Copeia, vol. for 1937, pp. 149–150.

SEABRA, ANTONIO MARIA D'ALBUQUERQUE

1891. Esboco biographico do excellentissimo senhor Dr. Jacques Wladimar de Bedriaga. 8 pp. Coimbra; Imprensa da Universidade.

SLYE, MAUD, JOHN OLIVER LA GORCE, G. KINGSLEY NOBLE, and BARRINGTON MOORE

1923. Mary Cynthia Dickerson, 1866–1923. Nat. Hist., 23:507–519, portr., illus.

SMITH, MALCOLM

1938. George Albert Boulenger, 1858–1937. Copeia, vol. for 1938, pp. 1–3, illus.

1947. Stanley Smyth Flower, 1871–1946. Copeia, vol. for 1946, pp. 185–187, portr.

1951. Frank Wall, 1868–1950. Copeia, vol. for 1951, pp. 113–114, portr.

WALDEYER-HARTZ, W. VON

1920. Gustaf Retzius. Anat. Anz., 52:261–268, portr.

WETMORE, ALEXANDER

1945. Biographical Memoir of Leonhard Hess Stejneger (1851–1943). Natl. Acad. Sci. Biogr. Mem., Vol. 24, 4th memoir, pp. 145–195, portr.

WETTSTEIN, OTTO VON, FR. MAIDL, and JOSEPH EISELT

1941. Franz Werner als Mensch und Forscher. Ann. Naturh. Mus. Wien, 51:8–53, portr.

WHEELER, WILLIAM MORTON

1899. George Baur's Life and Writings. American Naturalist, 33:15–30, portr.

WOOD, N. L.

1944. Raymond L. Ditmars; His Exciting Career with Reptiles, Animals, and Insects. x + 272 pp., illus. New York: Julian Messner, Inc.

ORNITHOLOGY

By CHARLES G. SIBLEY
Cornell University

THE FIRST HALF of our Century of Progress was, for ornithology, concerned almost entirely with systematics. Collections were growing, new species were still being described with frequency, and the description of the unknown multitude of subspecies had barely begun. Most attempts to interpret the sigificance of behavior met with failure because the necessary premises had not yet been developed.

The study of natural history was peculiarly typical of northern Europe. England and Germany produced a majority of the naturalists of the time. The expansion of the colonial empires of the European nations resulted in extensive travel and the establishment of many private fortunes. With the tradition established and the means available it was a logical consequence that the study of birds should prosper.

Knowledge of North American birds prior to 1850, was largely due to the work of Alexander Wilson, Charles Lucien Bonaparte, William Swainson, John James Audubon, and Thomas Nuttall. Others there were, but these five produced the most extensive publications and illustrations. With Audubon's death in 1851, the pioneer era in American ornithology came to a close.

By 1853 ornithology was past its infancy. Few indeed were the major areas of the earth from which collections had not found their way to Europe or America. In Germany Herman Schlegel had recently (1844a, 1844b) begun to employ trinomials to designate geographic races and in a country house in England Charles Darwin was quietly working on a book (1859) which was to initiate great controversies and provide the stimulus for intensified research in all fields of biology for the next century.

There is a curious parallel between the histories of two German clerics of the 1860's. Both Gregor Mendel and Bernard Altum were ahead of their time. The importance of Mendel's now famous work (1865) went unrecognized for over thirty years, while Altum's concept of territory (1868) was not "discovered" until after H. Eliot Howard (1920) had independently arrived at similar conclusions.

The last part of the nineteenth century was marked by numerous local faunal treatises, especially in Europe, and by the issuance of elaborate monographs on various groups of birds. At the halfway point in our century, Robert Ridgway (1901, p. 1) epitomized the prevailing viewpoint of the time when he wrote:

> There are two essentially different kinds of ornithology: *systematic* or *scientific*, and *popular*. The former deals with the structure and classification of birds, their synonymies and technical descriptions. The latter treats of their habits, songs, nesting, and other facts pertaining to their life-histories. . . . Popular ornithology is the more entertaining, with its savor of the wildwood, green fields, the riverside and seashore, bird songs, and the

many fascinating things connected with out-of-door Nature. But systematic ornithology, being a component part of biology—the science of life—is the more instructive and therefore more important.

The understanding of the true significance of what Ridgway called "popular" ornithology had to await the development of a firm foundation of physiological, psychological, and ecological research. These in turn depended heavily (the debt is all too seldom acknowledged) upon a foundation of systematics. It was inevitable that "scientific" ornithology and "systematics" should seem synonymous to Ridgway.

Even as Ridgway wrote, the revolution was starting. Mortensen was banding birds in Denmark, Selous in England had started his energetic advocacy of the study of the living bird, and Chapman in the United States was urging the partial substitution of the binocular for the shotgun.

Within the first decade of the present century banding began to solve problems concerning migration. Heinroth showed how behavior could be a clue to phylogentic relationship, and Howard helped to reveal the self-deceiving pitfall of anthropomorphism. The barrier between the "scientific" and the "popular," which seemed so clear to Ridgway, was beginning to disappear.

If any one year may be selected as a "turning point" it would fall close to 1920. Until then it was possible to function as an adequate ornithologist if one was versed in the systematics, distribution, and life histories of birds. The increase of interest in psychology and physiology at first concerned only a few. Most scientific zoologists saw only the shadow of the "bird lover" in ornithology. (Some still do!) The feeling that the study of birds was unimportant to the serious scientist prevailed. Since 1920 there have been great changes. Birds have come to be recognized as providing excellent material for the study of animal behavior and evolution. Many of the phases of ornithology which Ridgway had dismissed as "popular" are now among the most abstruse subjects of zoology. Indeed, these items compose an important group of factors contributing evidence of relationships. In 1953 it would be impossible to justify a division into "two essentially different kinds of ornithology." The effective avian systematist of today must be more than a mere cataloguer with an eye for variation. Behavior, ecological relationships, physiology, genetics, and even parasites are utilized as clues to phylogeny.

The recognition of evolution as the central theme of all biology has obliterated the sharply drawn boundaries between disciplines even as the same realization has shown the reality of the blurred lines between our arbitrary taxonomic categories.

Systematics and Evolution

Two factors were largely responsible for the taxonomic viewpoint of the mid-nineteenth century: the belief in the immutability of the species promoted a strictly morphological species concept, and collections were mostly too limited to reveal the full breadth of individual and geographic variation. The change in the point of view toward the first of these factors was to depend upon the acceptance of the evolutionary doctrine and was destined to be a matter for debate during most of the next century. As for the second factor, collections were already growing rapidly.

Taxonomic practices during the early nineteenth century were in accord with the concepts of the time. If a newly acquired specimen differed from the "type" of the most closely related known species it became the type of a "new species." Some authors described each variant as a new species, regardless of the degree or cause of the differences. As collections grew it became apparent that not all the "species" which were being described were of equal rank. The first attempt to reflect differences in the rank of forms below the species level was made by Carl Friedrich Bruch who proposed (1828) that "variations" be designated by a third name added to the Linnean binomial. Fourteen years later, on September 23, 1842, at the twentieth annual meeting of the Society of German Naturalists and Physicians, Bruch (1843) again expounded his ideas before the zoological section of the society. He used the term "subspecies" and again cited trinominal combinations. At this meeting Hermann Schlegel (b. 1804, d. 1884) was the presiding officer. Whereas Bruch had used ternary nomenclature to designate any relatively slight degree of departure from the "typical," Schlegel soon began to apply it only to geographic variants. His first use of trinominals was in 1844 in the "Aves" section of Siebold's *Fauna Japonica*. Schlegel, although the junior author (with C. J. Temminck), was responsible for the nomenclature and used such combinations as *Pandion haliaetus orientalis* (p. 13), *Otus scops japonicus* (p. 27), and *Podiceps rubricollis major* (p. 122). Schlegel also employed the trinominal in his critical review of European ornithology in 1844.

The use of trinominals found no protagonists in Europe, and it was in the United States that it first gained general acceptance among ornithologists. Spencer Fullerton Baird (b. 1823, d. 1887) had begun the detailed ornithological exploration of North America in 1850 when he became the assistant secretary of the Smithsonian Institution. The survey trips for the Pacific Railroad brought in large numbers of specimens and by 1858 Baird was able to recognize numerous examples of geographic variation in his series. The evidence for general rules of geographic variation was also found by Baird. He noted Bergmann's Rule (body size increases toward the north and decreases toward the south) and in 1859 pointed out that the same change takes place in accordance with changes in altitude in the same latitude. Baird also noted that in the southern parts of its range a species tends to show relative increase in bill size and that Pacific Coast specimens of many species were darker than those from inland localities. He was well aware of the tendency for the characters of adjacent differentiated populations to merge (i.e., intergrade) where the margins of their ranges adjoined. In 1858, with the cooperation of John Cassin and George N. Lawrence, Baird published the famous ninth volume of reports on the Pacific Railroad survey. Under Baird's skillful direction this volume became far more than a mere "report." It was in fact the most important treatise on the systematics and nomenclature of North American birds up to that time and remained so for many years.

It was Baird's protégé, Robert Ridgway (b. 1850, d. 1929), who next applied himself to the problem of the boundary between species and subspecies. When but seventeen years old Ridgway was appointed zoologist to the United States Geological Survey of the 40th Parallel. The expedition went to Panama by ship, crossed the Isthmus, then took another ship to San Francisco. For the next two years young Ridgway collected in the West, returning to Washington in 1869.

In that same year, in the second paper of his budding career, Ridgway proposed that, if two populations are extremely different, even though they are connected by a chain of intermediate forms, they should be considered full species. This concept showed the effects of the morphological species definition coupled with the dawning realization that geographic variation had to be taken into consideration.

One of the most able American biologists of this period was Joel Asaph Allen (b. 1838, d. 1921). In 1871 Allen demonstrated the correlation between coloration and humidity in birds, the darker populations being associated with high humidity, the lighter with aridity. He proposed that, instead of applying a name to each local population, species should be diagnosed in relation to the laws of variation. This was similar to von Gloger's (1833) suggestion. In 1877 Allen opposed the invocation of natural selection to explain the genesis of species in favor of a Lamarckian concept of the direct influence of temperature, humidity, food, etc.

Some of these developments hardly seem like "progress" when viewed from the vantage point of 1953, but they are evidence of the problems which were under attack by the systematists of the time, whose investigations were soon to produce more durable results.

In Elliot Coues (b. 1842, d. 1899) American ornithology found its genius. It was he who took the decisive step in the right direction. In 1872 in his famous *Key* he adopted the viewpoint that geographically complementary forms which were clearly closely related were subspecies of one species, regardless of the degree of difference between the extremes. Coues used the abbreviation "var." to indicate geographic races. The same system was employed by Baird, Brewer, and Ridgway in 1874 and remained in effect until 1881, when Ridgway took the final step to a true ternary nomenclature.

There was a vast difference between the viewpoint of Schlegel and that of Coues and Ridgway. The former believed in the constancy of species and used the trinominal to designate deviations from the "type" of the species. The Americans in contrast were stanch Darwinians and for them the third name served to identify an incipient species. Baird was their mentor and he believed that if the connecting links should become extinct the previously intergrading forms would develop into distinct species.

Remarkably enough there was virtual unanimity among the leaders in systematic ornithology in the United States regarding the concepts and usage of ternary nomenclature. Coues, the one among them with truly cosmopolitan views, decided to go to England to present the case for trinominalism and to urge the adoption of uniform rules. His optimism was not shared by Ridgway (Harris, 1928, p. 51), who felt that little would be gained. On July 1, 1884, Coues met with a group of the outstanding zoologists of England at the British Museum in South Kensington. As Ridgway had predicted, the proposals met with little enthusiasm. Only Henry Seebohm (b. 1832, d. 1895) recommended their acceptance but he was opposed by such potent adversaries as R. Bowdler Sharpe and P. L. Sclater. Coues returned home in defeat.

In 1885 the Committee on Nomenclature of the American Ornithologists' Union officially accepted the concept of Coues and Ridgway. The motto of the time was "intergradation is the touchstone of trinominalism."

In Europe the battle had barely begun. Seebohm (1887) had pointed out with keen insight that English ornithologists, while they accepted evolution in theory, were failing to utilize it as a working hypothesis. He urged the adoption of ternary nomenclature to differentiate nascent forms from "complete" species. Seebohm also was the first ornithologist to recognize the importance of isolation in species formation. He understood clinal variation and applied the subspecific concept solely to variation which could be defined geographically.

In Germany there were some who gave trinominalism a trial but, except for Ernst Hartert (b. 1859, d. 1933), their sponsorship was carefully qualified. In 1891 Hartert went to England and in 1892 he became the director of the Tring Museum, the remarkable private museum of Walter Rothschild (b. 1868, d. 1937). After Seebohm's death in 1895, Hartert was the only ornithologist in England consistently applying trinominals. Hartert expanded the subspecies concept to include slightly differentiated forms, even though actual intergrades were not present. Thus insular races were included in the concept and the requirement of intergradation was replaced with a biological interpretation of the situation in nature.

For several more years the advocates of ternary nomenclature were to be looked upon as traitors but gradually they gained disciples. By 1901 Hartert was joined by several authoritative workers, the most effective being Carl E. Hellmayr (b. 1878, d. 1934). In 1903, in the introduction to his mighty work on palearctic birds, Hartert defined subspecies as geographically separated forms of the same species which are characterized not by the minor degree of the differences between them, but by differences which are related to geographical separations.

The publication of Hartert's book marked the turning point, although both Sclater and Sharpe still held out. In 1909 Sharpe called the ternary system "destructive" and gloomily predicted that all zoologists who employed it would find themselves overburdened with names. He agreed that subspecies did occur in nature but held that the binary system was sufficient for all requirements. Putting his belief into practice Sharpe raised to full species all those forms described as subspecies and thereby attained the high number of 18,939 species in his *Hand-list* (5:xii, 1909). The discrepancy between that number and the recent count by Mayr and Amadon (1951) of 8,590 species is mostly due to the difference in application of the species concept.

By 1912 the battle was won. The *Hand-list of British Birds* (Hartert, *et al.*) used trinominals and caused little complaint. There followed a period of re-evaluation during which many species were suppressed to the rank of subspecies and descriptions of new subspecies appeared in increasing numbers. Now that the nomenclatural practice was established it was inevitable that improvements in the causal interpretation of geographic variation and its relationship to speciation would follow.

As early as 1900 Otto Kleinschmidt (b. 1870) had recognized that the new concept implied that each species was composed of geographically complementary forms. Kleinschmidt opposed the view that subspecies were incipient species and sought to bridge the gap between the adherents of the Linnaean species and those who believed in the nascent character of subspecies. His proposal of the term "Formenkreis," to designate a geographically complementary series of related forms was an attempt to emphasize the distinction between the new concept and the Linnaean species and to overcome the objections of those who refused to give up the binary system.

Kleinschmidt admitted the existence of organic evolution but believed that evolution had taken place within each *Formenkreis* following its special creation. In 1926 he elaborated upon the *Formenkreis* concept but the weaknesses imposed by his insistence on considering each "seed species" the result of special creation were sharply criticized. Bernhard Rensch (b. 1900) was the chief critic of Kleinschmidt's concept. Rensch (1929) clarified the concept by proposing that Hartert's geographically varying species should be called "Rassenkreise" and two or more closely related but monotypic species which are geographically complementary should be called "Artenkreise." These terms have not come into general usage but they served to call further attention to the characteristics of geographically variable groups.

The publication of *Genetics and the Origin of Species* (1937) by Theodosius Dobzhansky marked the beginning of a new phase in avian systematics. This book made a deep impression on naturalists by relating systematics to genetics. Dobzhansky was largely responsible for bringing to the attention of taxonomists the important developments in population genetics made by Sewall Wright in the United States and R. A. Fisher in England.

With the realization that studies of variation were capable of producing important evidence of evolutionary processes a new method of investigation developed. In 1941 Alden H. Miller (b. 1906) forcibly demonstrated the value of examining large series of specimens in the study of variation. In his study of the avian genus *Junco* Miller assembled 11,776 study skins. Special trips were made to critical areas to collect adequate numbers of birds and the analysis of variation utilized statistical techniques to indicate probable as well as observable ranges of variation. Miller's *Junco* paper has served as the inspiration and the pattern for a number of subsequent studies of speciation undertaken by his students.

Because of the relatively advanced state of avian systematics it was almost inevitable that an ornithologist would produce the first synthesized treatment of taxonomic practice and evolutionary theory. The synthesis was admirably provided in 1942 by Ernst Mayr (b. 1904). In his *Systematics and the Origin of Species* Mayr gave systematics the first adequate integration of taxonomy, genetics, and natural history. Mayr has continued to lead in the field of evolutionary systematics. He was the prime mover in the founding of the Society for the Study of Evolution in 1946, and the first editor (1947–1949) of the journal *Evolution*. The contributors to this journal have included botanists, geneticists, paleontologists, and zoologists, with a wide diversity of special interests. The existence of the Society and the journal epitomizes the modern synthesis of fields of thought which a few years ago were regarded as diverse disciplines. Further evidence of this synthesis is provided by the recent (1953) volume on methods and principles of systematic zoology coauthored by Mayr and the entomologists, Linsley and Usinger. For a review of speciation in birds and a bibliography of recent publications see Mayr, 1950.

The prediction by Sharpe in 1909 that ternary nomenclature would eventually overburden its users with names is currently finding new protagonists. The description of clinal variation is difficult to accomplish with names and excessive subspecific "splitting" has caused some systematists to propose that trinomials should be discarded or at least withdrawn from the protection of the International Rules of Zoological Nomenclature. Thus, in 1953, we see the beginning of a third phase in the description of geographic variation. Just as the recognition of geographic subspecies originally resulted from the combination of the development of evolutionary theory and the growth of collections so the present dissatisfaction results from the same factors. The theoretical basis has now, for continental situations at least, outstripped the descriptive method and collections are now large enough frequently to reveal the true details of clinal variation. It is yet too early to discern the outcome but the most hopeful approach will probably be found in a numerical evaluation of clines for only in numbers do we have a means for expressing or describing continuous variation. Although Sharpe's prediction thus proves to have contained a measure of truth, his advocacy of adherence to strict binomialism is certainly not the answer to the problem.

The Anatomy and Classification of Birds

The earliest systems of classification were based either upon external characters such as the bill and foot structure or upon characteristics of habit (swimming, running, etc.). The famous English anatomist, Richard Owen (b. 1804, d. 1892), devoted a number of papers to avian anatomy, and the second volume of his three-volume work on vertebrate anatomy (1866–1868) was concerned to a large extent with birds. Johannes Müller (b. 1801, d. 1858) proposed (1847) a division of the passerines upon the basis of the structure of the syrinx, a method still followed.

In 1867 Thomas Henry Huxley (b. 1825, d. 1895) developed a classification of birds upon the structure and relative positions of the palatal bones. The fallacy of attempting to base broad conclusions upon such a narrow basis was not immediately apparent and the palatal structure has been used by many subsequent workers as a basis for ordinal groupings. Recently (e.g., McDowell, 1948, and Hofer, 1949) there have been strong doubts cast upon the validity of Huxley's palatal types.

Alfred Henry Garrod (b. 1846, d. 1879) fell into similar difficulties when he based his classification primarily upon the arrangement of the carotid arteries (1873a) and certain pelvic muscles (1873b, 1874). His "pelvic muscle formula" has been used extensively and George E. Hudson has recently (1937) re-evaluated and extended Garrod's formula.

William A. Forbes (b. 1855, d. 1883) and Hans F. Gadow (b. 1855, d. 1927) produced a long series of reports on bird anatomy. Gadow (1891) wrote the section on avian anatomy for Brönn's *Klassen und Ordnungen des Thier-Reichs.* In this monumental work Gadow brought previous studies up to date and attempted to describe the complete morphology of the bird, including function and homologies. At about the same time (1888) there appeared the great two-volume work of Max Fürbringer (b. 1846, d. 1920), in which he assembled an enormous amount of anatomical information and carefully weighed the characters of value in classification. He recognized that the flightless groups were not necessarily monophyletic. Fürbringer's work is still the classic of bird anatomy.

To some opponents of Darwinism analogy and homology were of equal taxonomic rank. In 1885 E. F. von Homeyer (b. 1809, d. 1889) included the woodpeckers, nuthatches, creepers, and hoopoes in the same order, an arrangement similar to that used by Willughby more than two hundred years before! As late as 1893, Anton Reichenow (b. 1847, d. 1915) indicated his belief that a system of classification should be a means of identification and no more.

The careful work of Fürbringer and Gadow did much to overcome these viewpoints. In 1898 Frank E. Beddard (b. 1858, d. 1925), who had followed in the footsteps of Garrod and Forbes, published his volume on the structure and classification of birds, which brought together a great amount of the anatomical evidence for the arrangement of orders and families.

Descriptive anatomy languished somewhat after the turn of the century. In the United States Robert W. Shufeldt (b. 1850, d. 1934) continued to describe the osteology of birds and in England William P. Pycraft (b. 1868, d. 1942) produced an impressive series of anatomical papers.

In recent years the studies by George E. Hudson, Fred H. Glenny, and William J. Beecher have been directed toward the clarification of classification through anatomical research. Hudson has published (1937, 1948) studies on the muscles of the pelvic appendage; Glenny, beginning in 1940, has produced a series of papers on the main arteries in the region of the heart; and Beecher (1950) used the bill and jaw musculature to furnish evidence of convergent evolution in the American orioles. Other recent research has been concerned with the interpretation of functional and adaptational anatomy rather than its utilization in classification. The work of W. H. Burt (1930) on woodpecker adaptations, M. Stolpe (1932) on the hind limb, A. H. Miller (1937) on the Hawaiian goose, W. L. Engels (1940) on adaptations in the thrashers, F. Richardson (1942) on tree-trunk foraging birds, H. I. Fisher (1946) on the New World vultures and William J. Beecher (1951) on the American blackbirds, are examples of this trend.

Bird Migration

It was within the last half of the eighteenth century that the belief that some birds hibernated in the muddy bottoms of ponds and lakes was finally discredited. With the general acceptance of the fact that birds did actually migrate there came a wave of speculation as to the methods, routes, and significance of the migratory movements. Precise data based upon observations were few at first but gradually a body of reliable information was accumulated. Among the first reliable data were records of the arrival and departure of migratory species at a particular location. In 1828 Hermann Schlegel had speculated upon the routes and places of winter residence of European birds and the Swedish ornithologist Ekstrom had published the first arrival and departure dates of migratory species. In 1853, Karl E. Kessler, a professor at the University of Kiev, published the arrival and departure dates for a number of species at various localities in western Russia and compared the dates with temperature. In spite of these records of actual field observation, most of the investigations into migration were conducted from a desk. J. A. Palmén (b. 1845, d. 1919), a Finnish scholar, proposed a theory of "flyways" in 1876. He believed that there were nine narrow migratory lines which were followed by European and Asiatic birds. This concept was eventually disputed by E. F. von Homeyer (1881) who concluded that migratory birds merely followed a definite direction and that the members of a given species pass through Europe on a broad front, the width of which is equal to the width of the breeding territory. He also stressed that the migratory direction is northeast-southwest and that the "flyways" of Palmén were the result of birds being forced together into narrow flight lines in mountain passes or other topographic features.

Although some of his conclusions have been found in error, it was Heinrich Gätke (b. 1814, d. 1897) who gave the study of migration its greatest stimulus during the latter years of the nineteenth century. For fifty years he resided on the island of Helgoland and made observations on the hordes of migrants which paused there during the spring and fall flights. In 1891 he summarized the ideas gained from his half century of observation. Gätke agreed with von Homeyer that migration was on a broad front. He also developed the curious idea that some species which nested in Siberia reached their African wintering area by flying first west to England and then south to Africa. In the spring Gätke believed that they followed the hypotenuse of the triangle, northeast from Africa to Siberia.

Recognizing the need for cooperation, Anton Reichenow and a group of colleagues had (1875) called for help from all German ornithologists to fill gaps in the knowledge of German birds. Migratory routes were of special interest. Beginning in 1877 the results were published in the *Journal für Ornithologie*. The practice was soon copied in England, where a committee for the study of bird migration was formed. Its first report appeared in 1879. The Ornithological Society of Vienna founded a committee on ornithological observation in 1882 and in 1883 the American Ornithologists' Union appointed the Committee on Bird Migration at the first annual meeting of the Union. C. Hart Merriam was the first chairman of the committee.

These developments caused Rudolph Blasius and Gustav von Hayek of Austria to develop a plan for a world-wide network of ornithological observers. Crown Prince Rudolph of Austria commissioned them to organize the First International Ornithological Congress, which met in Vienna in 1884. Blasius became the chairman of a committee to organize the observers of the world and the publication *Ornis* was founded and first published in 1885. The undertaking did not succeed long. The mass of uncritically accepted data was of greatly variable value and no one was willing to undertake its analysis. By 1890 the various branches had again become autonomous.

In America the Committee on Bird Migration had enthusiastically set to work. Merriam's energy and knowledge had combined to push the project along. By 1885 the job had grown too large for the American Ornithologists' Union and in 1886, when Merriam became head of the Division of Economic Ornithology and Mammalogy, the migration studies were continued under governmental auspices. In 1888 Wells W. Cooke (b. 1858, d. 1916), who eventually became the "bird migration expert" of the Bureau of Biological Survey, published his classic report on migration in the Mississippi Valley. This paper attempted to correlate weather data with observations on migration and marked the beginning of such investigations in North America.

As valuable and important as these studies were, they were limited by the available data. Phenology did not provide information concerning the speed and direction of individual migrants; a new technique was needed.

Individual birds had been marked on many previous occasions but the attempts were sporadic and of short duration. It was a Danish schoolmaster, Hans Christian Cornelius Mortensen (b. 1856, d. 1921) who first attempted to band birds in a systematic fashion. His first trial in 1890 was with zinc bands inscribed "Viborg 1890." Two such bands were placed upon starlings. Mortensen noted that the bands seemed to be unpleasant to the birds and gave up the project. A few years later aluminum came into use for poultry bands. A merganser which Mortensen banded with one of these was shot soon after and the band was returned to him. In 1899 he captured and banded 162 adult starlings but no returns were received. The experiment was repeated in 1900 with bands stamped "M. Danmark" and this time his banded birds were shot in Holland and Norway. The technique had proved successful.

Banding developed rapidly. In 1900 the German Ornithological Society (Deutschen Ornithologen-Gesellschaft) subsidized and founded the now famous "Vogelwarte Rossitten." This bird observation station located at the town of Rossitten on the narrow coastal spit of the Kurische Nehrung was placed under the direction of Johannes Thienemann (b. 1863, d. 1938). The principal objective was the study of migration. Banding was begun in 1903, using aluminum rings carrying a number and the year. By 1937 over 763,000 birds had been banded at Rossitten and returns totaled more than 10,000. The Rossitten station remained active until World War II and produced a large number of significant papers. The idea of banding spread rapidly and was adopted by other organizations and individuals. Paul Bartsch (b. 1871) of the United States National Museum banded 101 fledgling black-crowned night herons near Washington, D. C., in 1902 and 1903, and in 1902 Leon J. Cole (b. 1877, d. 1948) proposed the systematic use of banding as a means of studying migration.

Other investigators soon followed these pioneers and by 1909 banding had become important enough to suggest the need for an organized effort. The American Bird Banding Association was formed in New York on November 8, 1909. For the next decade the work was sponsored by various organizations, including the Linnaean Society of New York and the New Haven Bird Club, in addition to the American Bird Banding Association. In 1920 the Bureau of Biological Survey took over the responsibility of furnishing bands and maintaining the records and Frederick C. Lincoln was placed in charge of the project. Over 1,000,000 birds had been banded in the United States and Canada by 1933 and nearly 6,000,000 by 1949.

The year 1909 also saw the formation of two banding organizations in Great Britain. A. Landsborough Thomson founded the Aberdeen University Bird-Migration Inquiry and Mr. H. F. Witherby launched a banding program in connection with the magazine *British Birds.* In 1937 the latter program was transferred to the control of the British Trust for Ornithology, with headquarters in the British Museum (Natural History). By 1927 there were seven European countries operating banding stations. In 1950 Rydzewski listed banding stations in eighteen European countries, Egypt, South Africa, India, Japan, Australia, New Zealand, Canada, and the United States.

The German bird observation stations of Rossitten and Helgoland have moved to new locations since World War II. The Rossitten group, under Ernst Schüz, is now at Radolfzell on Lake Constance, while the Helgoland station has moved to Wilhelmshavn and is directed by Rudolf Drost. The first bird observation station in Sweden was founded at Ottenby in 1945 and others (e.g., Fair Isle, Isle of May, Skokholm) have been intermittently active in the British Isles.

The information derived from banding includes much in addition to data concerning migratory routes. Knowledge of the dispersal of juveniles, sex ratios, speed of flight during migration, longevity, plumage change in relation to age, and diseases and parasites are among the items to which banding has made a direct or indirect contribution.

Thanks to the banding technique the mysteries of bird migration were fewer in 1920 than they had been in 1900, but at least two major problems remained unsolved. What was the stimulus which started a bird off on its migratory flight with such remarkable precision, and how did the migrating bird find its way? These questions demanded experimental investigation. The precision with which migratory birds arrived at a given point year after year was proof that the timing device which provided the stimulus was equally precise. The annual cycle of weather, seasonal variation in food supply, and other phenomena had been suggested as the source of the stimulus. These were too variable to account for the regularity of migration. When Professor William Rowan of the University of Alberta began his investigation into the problem, he had logically settled upon the annual cycle of changing day-length as the only apparent cyclic phenomenon with the necessary degree of precision. This hypothesis he set out to test. In the fall of 1924 Rowan trapped southbound slate-colored juncos passing through Edmonton. The birds were caged in outdoor aviaries, one of which contained an electric light. The experimental procedure was classically simple. Beginning on November 1 the light in the experimental cage was left burning for 7½ minutes after dark. A daily increment of 7½ minutes was added until December 3, when the increment was reduced to 5 minutes. By December 15 this procedure resulted in the light remaining on until 11:00 p. m. The increases were then discontinued, the light going out at 11:00 p. m. until January 9, when the experiment was terminated. Although their environment was that of a Canadian winter the gonads of the experimental birds had attained the maximum breeding size, and the males were in full song. The gonads of the control birds in the unlighted cage were at the winter minimum size. Here indeed was proof of the effect of photoperiodism on the sexual cycle. Rowan's little book *The Riddle of Migration* (1931) summarizes his experiments. Although some of Rowan's conclusions concerning the relationship between the gonad cycle and the migratory impulse have been modified, his experiment started the intensive investigations, such as those of Wolfson (1945), which have led to an understanding of the annual stimulus for migration. The present state of knowledge has been summarized by Farner (1950), who proposes a working hypothesis which attempts to reconcile many seemingly divergent facts and suppositions. This hypothesis, somewhat simplified, states that twice each year migratory species of birds come into a distinct physiological condition which places the bird in a "disposition to migrate." This is indicated by the deposition of fat in many species. The gonads begin to increase in size and a condition of "restlessness," which is especially noticeable in caged birds, is evident.

The fundamental cycle which periodically places the bird in the "disposition to migrate" is probably the result of the cyclic function of the anterior lobe of the pituitary gland. This cycle could be, and probably is, the result of periodic change in stimulation by periodic external environmental factors such as day-length. When a certain threshold of stimulation is reached, the bird is stimulated to migrate. The act of migration, that is, the actual movement through space on a remarkably exact time schedule, is the result of a complex inherited behavior pattern stereotyped in the nervous and endocrine systems.

The problem of orientation and navigation during the migratory flight posed a still more difficult problem. The classical experiments of J. B. Watson and K. S. Lashley (1915) had proved that nesting birds could find their way "home" over long, unfamiliar routes. Further experiments on homing have been carried out by Rüppel in Germany, Lockley in England, and Griffin in the United States. All tended to confirm the fact of homing ability in birds but failed to yield unquestionable proof of the method of orientation. The importance of landmarks in the homing of carrier pigeons was established by several workers, including the Heinroths (1941).

The hypotheses presented by Ising (1945) and Yeagley (1947), postulated that orientation could be achieved by detection of variations in the fields of force resulting from the earth's rotation (Coriolis force) were vigorously attacked by both physicists and biologists (see Odum, 1948).

The most promising development in the field of orientation research is the work of Gustav Kramer (1949, 1950), who has successfully demonstrated that the sun is utilized in orientation at least by certain diurnal migrants. Kramer constructed a round cage having six equally spaced windows. Each window was equipped with a hinged shutter upon which a mirror was mounted. By manipulation of the shutters the angle of the sun's rays entering the cage could be modified. With the shutters wide open a spring migrant European starling (*Sturnus vulgaris*) made repeated attempts to fly toward the northwest, the normal direction for the spring migration. When the mirrors were placed so as to deflect the direction of the incidental light by 90° the captive bird changed the direction of its flight in accordance with the direction of the light.

There still remains the problem of orientation by nocturnal migrants but Kramer's experiment will certainly direct further research along profitable pathways.

The paper by Drost (1950) provides a review of much of the recent work on bird migration.

Bird Behavior

The necessity of objectivity as a component of the scientific method is undeniable. It is equally certain that no field of endeavor has had a more difficult time incorporating the objective viewpoint into its investigations than that of animal behavior. Not until it emancipated itself from the burden of anthropomorphism was it able to attack its problems with any measure of success.

The viewpoints of Christian Ludwig Brehm (b. 1787, d. 1864) and his son Alfred Edmund Brehm (b. 1829, d. 1884) dominated the thinking on bird behavior during the mid-nineteenth century. The younger Brehm's two great works, *Das Leben der Vogel* (1861) and *Illustrirtes Thierleben* (1864–1869), went through several editions and were translated in various degrees into other languages. Brehm's viewpoint was strongly anthropomorphic and sentimental and, since his influence was great, he was accepted as authoritative. The first serious challenge to Brehm's views was presented by Bernard Altum (b. 1824, d. 1900) in his now famous classic, *Der Vogel und Sein Leben* (1868). Altum's viewpoint was anti-Darwinian but also anti-anthropomorphic. He proposed a strongly instinctive mode of behavior for birds and believed that their activities were the result of unthinking reactions to external stimuli.

Altum's fame is secure as the first to expound the concept of territory in birds, if for no other reason. His discussion of territorial behavior includes an analysis of the function of song as a threat to other males and an invitation to females and the importance of territory in reducing competition for food between members of a species. (For a review of Altum's territorial concept see Mayr, 1935.)

The reaction to Altum's ideas was immediate and mostly hostile. Brehm's influence was so great that it was twenty-five years before Altum's views were generally accepted in Germany.

Despite the seemingly revolutionary and advanced concepts expressed by Altum he did not attract much attention outside of Germany and even there the importance of his ideas was not fully realized. This situation was probably due to the general lack of interest in psychological problems among ornithologists during the latter part of the nineteenth century.

Progress came slowly, and for some time it was not due to the work of ornithologists but to the investigations of psychologists and general biologists. The work of C. Lloyd Morgan (b. 1852, d. 1936) was unnoticed by most ornithologists but gradually his ideas concerning instinctive behavior became known to a few. Morgan's theory of instinctive behavior (1896) was basically mechanistic and was founded in Darwinism. He believed that instincts are innate and that they become fixed by selection. He also found reason to believe that an instinctive chain of acts could be modified through the conscious activity of the animal and he called this type of modification an "acquired instinct." According to Morgan, an animal inherited a basic set of instincts but was able to learn by experience and add to its innate instinctive behavior.

As the concepts of psychology developed, a number of ornithologists began to apply them to the study of living birds. In the United States Francis H. Herrick (1901) was among the first to utilize photography and careful observation of the living bird in studying behavior. He emphasized that nest-building and other avian activities are purely instinctive acts in which the bird exhibits no power of choice. Arthur A. Allen's study (1914) of the red-winged blackbird *(Agelaius phoeniceus)* was an important milestone in avian ecological and life history research which influenced and set the pattern for numerous studies of single species by his students and other workers. In England the study of the living bird found an able and articulate protagonist in Edmund Selous (b. 1858, d. 1934). His books, *Bird Watching* (1901), *Bird Life Glimpses* (1905), and *The Bird Watcher in the Shetlands* (1905b), promoted the value of the notebook and binocular as tools of ornithology. His philosophy was amusingly presented in verse when he wrote:

> Some men have strange ambitions. I have one:
> To make a naturalist without a gun.

Selous correctly pointed out that there was little information available on birds except about their plumages, nests, eggs, and distribution. He stressed the need for studies of behavior and the need for interpretation of habits, in addition to mere factual recitation. His viewpoint was Darwinian and his interpretations of behavior were in terms of selection and survival.

Two years later, H. Eliot Howard (b. 1873, d. 1940) began his studies of the British warblers (1907–1915). Howard was concerned primarily with the investigation of nesting and brood care. His study of the several species of British warblers permitted comparison of the breeding biology of a group of closely related species. In 1910 Howard called attention to the fact that the males in many species took up a territory and defended it against intruders. He developed the territorial concept, apparently unaware of the work of Altum (1868), and in 1920 devoted an entire volume, *Territory in Bird Life,* to the subject. Howard's carefully documented theory had an immense effect on the ornithologists of the entire world. Others had recognized the general facts and had even stated the elements of the theory of territory but Howard's emphatic presentation became the starting point of a new era in the study of avian behavior. Among the many important studies which have utilized and expanded the territorial concept since 1920 are two which rank as classics. As a result of several years of intensive work on the song sparrow (*Melospiza melodia*) near Columbus, Ohio, Margaret Morse Nice published two volumes (1937, 1943) dealing with its life history and behavior. Mrs. Nice's familiarity with the literature of avian behavior permitted a truly comparative presentation and her methods have served as the model for numerous subsequent investigations. In 1941 Mrs. Nice prepared a valuable review of the territorial concept which includes a comprehensive bibliography of the subject.

The well-founded tradition of field natural history characteristic of present-day England, begun by Gilbert White (1789) and nurtured by Edmund Selous, is today led by David Lack. Lack's fine study (1939) of the life history of the English robin (*Erithacus rubecula*) utilized the techniques of observation of marked individuals (color-banded) and the experimental use of stuffed specimens. His work served to focus attention on the value of the intensive study of single species.

The first to bridge the gap between behavior and systematics was Oscar Heinroth (b. 1871, d. 1945), who presented the idea (1910) that voice and behavior were clues to relationship. Heinroth's interest was in the living bird and many of his behavior studies were on captive birds in the Berlin Zoo. Heinroth laid the foundation for further research in comparative behavior and crowned his life's work with the remarkably detailed three-volume work, *Die Vogel Mitteleuropas* (1924–1928), with his wife as coauthor. This ambitious project was in preparation for twenty years and included nearly three thousand photographs and descriptions of the details of behavior, development, and other phases of life history.

The study of instinctive behavior received a new impetus with the work of Konrad Lorenz in the 1930's. At his home in Altenberg, Austria, Lorenz studied free-living, semitame birds of several species. His work on the behavior of the jackdaw (*Corvus monedula*) started in 1925 with a single bird. A flock was gradually built up which provided research material for a number of ethological studies (e.g., 1931). In 1935 Lorenz proposed the "releaser" concept to explain the initiation of instinctive behavior patterns. In an English version of the 1935 paper Lorenz (1937, p. 249) defined a "releaser" as follows.

> The means evolved for the sending out of key-stimuli may lie in a bodily character, as a special color design or structure, or in an instinctive action, such as posturing, "dance" movements and the like. In most cases they are to be found in both, that is, in some instinctive acts which display color schemes or structures that were evolved exclusively for this end. All such devices for the issuing of releasing stimuli, I have termed *releasers* (*Auslöser*), regardless of whether the releasing factor be optical or acoustical, whether an act, a structure or a color.

The releaser concept found general acceptance among students of behavior and was quickly applied to other studies. It was the unifying principle which had been lacking and which greatly simplified much of the complicated terminology that had enmeshed the study of animal behavior. Owing largely to Lorenz the problem of innate behavior has received a great deal of attention in the past fifteen years.

There have been many ethological studies utilizing the "releaser" concept. The principal contributor has been Nikolas Tinbergen, formerly of the University of Leiden, now Lecturer in Animal Behavior at Oxford. Tinbergen has successfully developed the objectivistic approach to the analysis of animal behavior. His work has included study of the orientation mechanism of the digger wasp (*Philanthus*), territory and breeding behavior of the three-spined stickleback (*Gasterosteus aculeatus*), and numerous investigations of avian behavior. Among the latter his study (1939a) of the spring behavior of the snow bunting (*Plectrophenax nivalis*), and the analysis of the releaser for the begging response in herring gull (*Larus argentatus*) chicks (with H. C. Perdeck, 1950) are examples. Tinbergen's ability to synthesize has been of great value to other ornithologists. His extensive knowledge of this complex field has made possible several valuable "review" papers (1936, 1939b, 1942, 1948) and recently (1951) has resulted in a book which summarizes the present state of knowledge of instinctive behavior.

Fossil Birds

The history of paleornithology is nearly coterminal with the span of our Century of Progress. Few discoveries of importance were made before 1861, when the remains of *Archeopteryx* were found in the lithographic limestone quarry at Solenhofen, Bavaria. The skeleton of this Upper Jurassic link between reptiles and modern birds was described by Owen in 1863. In 1877 a second Jurassic bird was found near Eichstatt, Bavaria. It was described by Dames in 1884 as *Archeopteryx siemensi.* In 1921 Petronievics made this second fossil the type of the genus *Archeornis.* Both specimens combine numerous reptilian characters with the presence of feathers. There is general agreement that these Jurassic fossils represent the first birds although Lowe (1944) believes that they should be considered flying reptiles.

In the preparation of his four volumes on the fossil birds of France (1867–1871) Alphonse Milne-Edwards (b. 1835, d. 1900) visited all the large geological collections in Europe. He assembled more than 4,000 fossil bones and the skeletons of nearly 800 species of living birds for comparison. The illustrations are accurate enough to serve as the basis of comparison by critical modern workers.

The first important contribution to the study of fossil birds in America was made in 1870 by O. C. Marsh (b. 1831, d. 1899). In 1872 Marsh announced the discovery of the Cretaceous toothed bird, *Hesperornis regalis.* Marsh continued to describe avian fossils and in 1880 published a monograph on the Cretaceous toothed birds of North America. Marsh described a total of 40 species of fossil birds during his lifetime.

Edward Drinker Cope (b. 1840, d. 1897), Marsh's famous rival, described his first avian fossils in 1871 and the giant Eocene *Diatryma* from New Mexico in 1876.

One of the most prolific writers on osteology and paleornithology was Robert W. Shufeldt (b. 1850, d. 1934). In 1891 he began his descriptions of fossil birds, which were to number 43 species, more than the total of any other North American worker to date.

In South America, Florentino Ameghino (b. 1854, d. 1911) described (1891) the gigantic flightless Miocene bird *Phororhacos,* which stood at least seven feet tall and had an enormous raptorial beak. In 1895 Ameghino's book on the fossil birds of Patagonia appeared.

From the lower Eocene beds near Croyden, England, E. T. Newton described (1886) a huge flightless bird, *Gastornis,* larger than an ostrich, which may be related to the ducks and geese (Swinton, 1934).

Most of the avian fossils discovered before 1909 were those of large, flightless species. This is not surprising, for flying birds are less likely to become ensnared in natural traps and the bones of small birds are so fragile as to reduce the chances of intact preservation in ordinary sediments. In 1909 Loye Holmes Miller began the study of the abundant Pleistocene material preserved in the asphalt traps of Rancho La Brea, McKittrick, and Carpenteria in southern California. Among the numerous bones of large raptors and scavengers were thousands of skeletal elements belonging to small passerines. As a result of the studies by Loye Miller, and later by Hildegarde Howard and Alden Miller, the Pleistocene avifauna of California is the most completely known fossil avifauna in the world. From Rancho La Brea alone 105 species have been identified.

Since 1920 the most active paleornithologist in North America has been Alexander Wetmore. In 1921 he described an owl from the Eocene of Wyoming and has since described a number of Tertiary birds, primarily from the Miocene and Pliocene. His check-list (1940) of the fossil birds of North America includes 165 forms which are still living and 184 extinct species. This list has increased but slightly since 1940.

Two valuable references to avian fossils have appeared in recent years. In 1926 Gerhard Heilmann's *The Origin of Birds* presented the results of his studies on the relationships between reptiles and birds. Heilmann amassed anatomical and embryological evidence to support the idea of the reptilian origin of birds. His book contains valuable and detailed studies on *Archeopteryx* and *Archeornis.*

The *Handbuch der Palaeornithologie* (1933) by Kálmán Lambrecht provides a review of the world-wide knowledge of fossil birds.

One consequence of the development of knowledge of fossil birds has been speculation as to the origin of flight. Marsh (1880) suggested a tree-dwelling ancestor while Nopcsa (1907) derived flying birds from rapid-running ground-dwelling forms. Beebe (1915) proposed the "tetrapteryx" stage as an ancestral intermediate form. This hypothetical progenitor had a "pelvic wing" which Beebe believed to be indicated by the femoral tract of modern birds. Steiner (1917) proposed a proavian which is both tree-dwelling and running, with long hind limbs and forelimbs equipped with functional claws and an expanded air-foil of feathers.

Two recent papers by Hildegarde Howard (1947, 1950) present evidence of avian evolutionary history based on the fossil record while Wetmore (1950) has reviewed the addition to the knowledge of fossil birds since the publication of Lambrecht's book in 1933.

Ornithological Periodicals

It is doubtful if any other class of animals has been the inspiration for the founding of as many serial publications as birds. Most of these journals have enjoyed but a brief life and few have become scientifically important. A small number have been privately printed; most have been or are the organs of societies or institutions.

Within the pages of the *Journal für Ornithologie,* the *Ibis,* and the *Auk* have appeared more than half the basically important ornithological papers of the past century. These three have enjoyed the benefits of an active membership in the supporting societies and that all-important necessity, good editorship over long periods of time.

It was partly as a protest against the provincialism of other ornithological periodicals that Gustav Hartlaub (b. 1814, d. 1900) and Jean Cabanis (b. 1816, d. 1906) founded the *Journal für Ornithologie* in 1852. With Cabanis as editor and leading German ornithologists as contributors the "J. f. O." soon became the principal German ornithological periodical. The present editor is Erwin Stresemann.

In 1858 the *Ibis* was founded in England as the organ of the British Ornithologists' Union. It too enjoyed a series of competent editors and quickly became the premier ornithological periodical in English. Among its editors have been Alfred Newton, Osbert Salvin, Philip Lutley Sclater, and his son, William Lutley Sclater. The present editor is R. E. Moreau.

The Nuttall Ornithological Club was organized in Cambridge, Massachusetts, in 1876 and began publication of *The Bulletin of the Nuttall Ornithological Club* in the same year. Seven years later, when the American Ornithologists' Union was organized in New York (September 26, 1883), the Nuttall Club offered its *Bulletin* and its editor as the foundation for the journal of the union. *The Auk* was chosen as the name of the new journal and J. A. Allen continued as editor until 1912, when he was succeeded by Witmer Stone. Glover Morrill Allen followed Stone in 1937. Following in succession as editor were John T. Zimmer, Harvey I. Fisher and Robert W. Storer (incumbent).

The official date of the founding of the Wilson Ornithological Club is December 3, 1888, although its roots go back to 1858 under various names. In 1889 a journal was started, the *Ornithologists and Oologists' Semi-Annual.* Within the next nine years the name was changed no less than six times, the seventh (1898), being *The Wilson Bulletin,* which survives today. At first devoted primarily to the field ornithology of the Middle West it has more recently included papers of wide scope and high quality. Among its editors have been Lynds Jones, Thomas C. Stephens, and Josselyn Van Tyne.

The Cooper Ornithological Club was organized on June 22, 1893. The *Bulletin of the Cooper Ornithological Club* began publication in 1899; in the following year the name of the journal was changed to *The Condor.* As editor from 1906 to 1939, Joseph Grinnell was largely responsible for its continuing success. His high standards have been continued by Alden H. Miller. In 1952 the name of the organization was officially changed to *Cooper Ornithological Society.*

The following list includes a world-wide representation of the periodicals devoted entirely to ornithology.

Aquila, founded 1894 in Hungary. Printed in both Hungarian and German.

The Emu, founded in 1900 as the official organ of the Australasian Ornithologists Union. (Australia.)

British Birds, founded in 1907. Devoted primarily to the occurrence and behavior of the birds of Great Britain.

Tori, founded in 1915 as the bulletin of the Ornithological Society of Japan. In Japanese.

El Hornero, founded in 1917 by the Ornithological Society of La Plata (Argentina). The principal ornithological journal of South America. In Spanish.

L'Oiseau, founded in 1920, and *Alauda* (1929) are the principal periodicals of France.

Le Gerfaut (1909–1914, 1919–), published by the Belgian Central Ornithological Society. In French.

The Ostrich (1930), journal of the South African Ornithological Society. Austin Roberts was the first editor.

Bird-Banding (1930), published by the Northeastern Bird-Banding Association (New England region). Includes reviews of the literature of avian biology.

Der Vogelzug (1930–1943), devoted primarily to studies of bird migration and published by the German bird observation station at Rossitten (Vogelwarte Rossitten). Publication suspended in 1943 during World War II. In 1948 the publication *Die Vogelwarte* replaced *Vogelzug* as the organ of the German bird observation stations.

Ornis Fennica (1924), published by the Ornithological Society of Finland. Papers in Finnish, German, or Swedish.

Ardea (1912), published by the Netherlands Ornithological Society.

Limosa, founded in 1928 as the *Orgaan der Club van Nederlandsche Vogelkundigen.* Became *Limosa* in 1937.

The preceding list includes some of the more enduring and important periodicals which contain only ornithological papers. In addition, many papers dealing with birds regularly appear in such journals as the *Proceedings* of the Zoological Society of London, *Evolution,* and the journals of psychology, physiology, anatomy, etc., in all languages.

The "occasional papers," "proceedings," "transactions," "novitates," "comptes rendus," "archives," etc., of museums and universities are other important sources of ornithological literature.

The *Zoological Record* is undoubtedly the most nearly complete bibliographic reference source for zoological literature. The "Aves" section averages nearly 1,500 references per year. It is certain that well over 100,000 books and papers on birds have been published during our Century of Progress.

Ornithological Monographs

The results of most original research today are customarily published in the periodical journals. This material is often widely scattered and frequently unavailable or unknown to many interested persons. Fortunately, it is also customary for specialists to synthesize the numerous research papers and to produce books which summarize their fields of endeavor. In ornithology there are innumerable books dealing with the distribution and occurrence of the birds of areas ranging in size from a university campus to the world itself. These vary from mere lists to extensive compendia containing enormous amounts of information. There have been far fewer books devoted to such subjects as behavior, anatomy, and other phases of avian biology.

Books which fall into these categories number in the thousands. Rather than try to cite numerous examples and thereby omit reference to many equally worthy of inclusion, it seems better to single out a few major works published before 1900 and to give more space to the important volumes of the past fifty years. Volumes which have been noted elsewhere in this chapter will not usually again be cited.

The general faunistic works on European birds are seemingly endless. The British Isles have been especially prolific of local faunal compilations. Following in the footsteps of William Yarrell (b. 1784, d. 1856), whose *History of British Birds* (1837–1843) was long the standard, was Howard Saunders (b. 1835, d. 1907), who brought Yarrell's work up to date in 1889 and further revised it in 1899. Today the standard work is the five-volume *Handbook* of H. F. Witherby and his collaborators (rev. ed., 1943). This remarkable compilation has no parallel in English but is in some ways comparable to the work of the Heinroths (1926–1928) on central European birds. Germany, too, has produced a spate of faunal treatises. Niethammer's recent (1937–1942) three-volume handbook is outstanding.

For Europe in general there is the magnificant nine-volume treatise by Dresser (1871–1890) and Hartert's (1903–1923) scholarly three volumes on palearctic birds.

African birds have been the subject of numerous books. Hartlaub (1857), Finsch and Hartlaub (1870), Shelley (1896–1912), Bannerman (1930–1951), and Chapin (1932–1939) are among the many contributors.

The English extended their interest in natural history to all parts of the British Empire. The ornithological volumes of *The Fauna of British India* (1889–1898) were prepared by E. W. Oates and W. T. Blanford. In 1922 E. C. Stuart Baker published the first volume of a revised edition of this work.

Australian birds were first extensively described in a monograph by John Gould (b. 1804, d. 1881), whose seven volumes (1840–1848) were illustrated with 600 hand-colored plates and followed by a supplement containing 81 more (1851–1869). In spite of his unfortunate prolixity for generic splitting the work of Gregory H. Mathews (b. 1870, d. 1949) is pre-eminent in Australian ornithology. His twelve large volumes (1910–1928) are among the last of the elaborately illustrated extensive faunal monographs.

The birds of New Zealand were treated by Walter L. Buller (b. 1838, d. 1906) in 1872–1873 and more recently (1930) by W. R. B. Oliver.

The avifaunas of most Asiatic countries have been treated in monographs. Many of these are listed by Casey Wood in his *Introduction to the Literature of Vertebrate Zoology* (1931, pp. 77–78).

Among the numerous faunal works on New World birds is the detailed systematic treatment of the birds of North and Middle America (1901–1950) by Robert Ridgway (b. 1850, d. 1929), which has been continued since Ridgway's death by Herbert Friedmann. In 1918, Charles B. Cory (b. 1857, d. 1921) began the publication of an extensive catalogue of all of the species and subspecies of the Americas and adjacent islands. This work was continued by Charles E. Hellmayr (b. 1878, d. 1944) after Cory had completed two volumes. The last four of the fifteen volumes were finally finished by H. B. Conover from Hellmayr's manuscript.

The "Aves" volumes of the *Biologia Centrali-Americana* (1879–1904) by Salvin and Godman described over 1,400 species of Central American birds. The authors, opponents of trinominal nomenclature, maintained a consistently binominal treatment in their work. Among more recent systematic treatments of Central American birds is that of Dickey and van Rossem on El Salvador (1938).

The books by Sclater and W. H. Hudson (1888–1889) and by W. H. Hudson (1920) on Argentine birds are among the best known of many volumes on South American birds. Among recently active workers have been John T. Zimmer on Peruvian birds (1931, *et seq.*) and William H. Phelps and William H. Phelps, Jr., mainly on the birds of Venezuela.

To date there has been only one attempt to describe all of the known species of birds in the world. It was the indefatigable Richard Bowdler Sharpe (b. 1847, d. 1909) who set this as his task shortly after he succeeded G. R. Gray as keeper of the bird collection of the British Museum (Natural History) in 1872. The first volume of the *Catalogue of the Birds in the British Museum* appeared in 1874. Of its twenty-seven volumes Sharpe himself wrote fourteen. Among others who contributed volumes to this remarkable undertaking were P. L. Sclater, G. E. Shelley, T. A. Salvadori, O. Salvin, and E. Hartert. These volumes include plumage descriptions, synonyms, references, and distributional information.

Sharpe's *Hand-list* (1899–1909) was also the first world-wide check-list. In 1931, James Lee Peters (b. 1889, d. 1952) published the first volume of his *Check-list of Birds of the World,* seven volumes of which had been completed by 1951. In terms of numbers of species this is approximately the halfway point.

Elaborately illustrated monographs of genera, families, or orders were produced in numbers during the latter part of the nineteenth century. John Gould (b. 1804, d. 1881) wrote and illustrated a number of famous works of this nature including the hummingbirds (1849–1861), which occupied five volumes and contained 360 colored plates. Otto Finsch (b. 1839, d. 1917) wrote a monograph on the parrots of the world (1867–1868), which is still the most complete account of the group. In the United States, Daniel Giraud Elliot (b. 1835, d. 1915) has published monographs on the grouse (1864–1865), the pheasants (1870–1872), the hornbills (1877–1882), the North American shore-birds (1895), and several other groups.

More recent monographic treatment has been accorded the pheasants by Beebe (1918–1922) and by Delacour (1951), the birds of prey by Swann and

Wetmore (1924–1945), and the ducks by Phillips (1922–1926). Murphy's two volumes on the oceanic birds of South America (1936) include extensive material on life history and behavior in addition to taxonomic and distributional data.

The thick volume by Knowlton (1909) is the only attempt to date to provide a survey of the habits, appearance, and distribution of the birds of the entire world. All families are considered with attention given to significant species in each. Newton's *Dictionary of Birds* (1893–1896) is an alphabetically arranged compendium of various phases of ornithology.

In marked contrast to the enormous number of volumes dealing with faunal or systematic groups is the paucity of works on avian biology. This situation is partly due to the fact that systematics must precede studies of the living animal and it is only recently that the classification of birds has attained the necessary degree of completeness. A second factor is the relative novelty of the basic concepts upon which interpretations of behavior, physiology, etc., are founded.

Among the first books which tried to bring together the information on bird biology were those of Beebe (1906) and Pycraft (1910). In 1923, J. A. Thomson published his volume on bird biology, which included chapters on adaptation, behavior, migration, and so forth.

The major work on avian biology to date was written by the dean of world ornithologists, Erwin Stresemann (b. 1889) and published (1927–1934) as a volume of Kükenthal and Krumbach's *Handbuch der Zoologie*. This monumental book contains extensive discussions of anatomy, physiology, and other phases of avian biology. Before Stresemann's volume was completed, there appeared the first parts of Franz Groebbel's (b. 1888) detailed treatment of avian anatomy and biology (1932–1937).

In 1950 a collaborative effort by a group of twelve French biologists under the direction of Pierre Grassé produced a volume which, while variable in the extent and quality of the treatment of its different sections, is the only readily available up-to-date compendium on the biology of birds. It contains chapters on anatomy, physiology, genetics, behavior, embryology, ecology, etc., and a systematic synopsis of the birds of the world.

Of importance to students of avian biology are such volumes as Friedmann's studies on social parasitism in the cowbirds (1929) and the parasitic cuckoos of Africa (1948), the compendium by Armstrong (1947) on bird behavior and N. Tinbergen's recent (1951) book on instinct. The book on bird parasites by Miriam Rothschild and Theresa Clay (1952) brings together for the first time the large and scattered literature on this subject.

Anyone familiar with the literature of ornithology will think of numerous works, as important as some herein included, which have been omitted. The attempt has been to select examples, not to survey the entire literature of the past century.

It has not been possible in this brief survey of ornithology during the past century to cover all of the aspects of the subject. Omission of such important phases of research as bird flight, avian genetics, ecology, endocrinology, and other subjects is regretted. For the reader interested in further historical information there is the recent and scholarly volume by Erwin Stresemann (1951), which has provided the foundation for several sections of this chapter. The debt to Professor Stresemann is gratefully acknowledged. The little volume by Maurice Boubier (1925) was also useful, as were the chapters in *Fifty Years' Progress of American Ornithology, 1883–1933* published by the American Ornithologists' Union on its fiftieth anniversay. Casey Wood's (1931) survey of the vertebrate literature and R. M. Strong's (1939–1946) bibliography were repeatedly consulted.

To my colleague and friend, Dr. William Graf, I owe a debt of gratitude for his patient and extensive help with the translation of large portions of Dr. Stresemann's book.

LITERATURE CITED

Allen, A. A.

1914. The Red-winged Blackbird: A study in the ecology of a Cat-tail marsh. Proc. Linn. Soc. New York, No. 24.

Allen, J. A.

1871. On the mammals and winter birds of East Florida, with an examination of certain assumed specific characters in birds, and a sketch of the bird-fauna of eastern North America. Bull. Mus. Comp. Zool., 2:161–450.

1877. The influence of physical conditions in the genesis of species. Radical Review, 1:108–140; reprinted in Ann. Rept. Smithson. Inst., 1905:375–402.

Altum, B.

1868. Der Vogel und sein Leben. 240 pp. Munster.

Ameghino, F.

1891. Enumeración de las aves fósiles de la Republica Argentina. Rev. Argentino Hist. Nat., 1:441–456.

1895. Sur les oiseaux fossiles de Patagonie. Bol. Inst. Geog. Argentino, 15:501–602.

Armstrong, E. A.

1947. Bird Display and Behaviour. iii + 431 pp. London: Lindsay Drummond.

Baird, S. F.

1859. Notes on a collection of birds made by Mr. John Xantus, at Cape San Lucas, Lower California, and now in the museum of the Smithsonian Institution. Proc. Acad. Nat. Sci. Phila., 11:299–306.

Baird, S. F., T. M. Brewer, and R. Ridgway

1874. A History of North American Birds. 3 vols. Boston: L. H. Brown and Co.

Baird, S. F., J. Cassin, and G. N. Lawrence

1858. Pacific Railroad Reports. Volume IX, Birds. lvi + 1005 pp. Washington, D. C.

Baker, E. C. S.

1922–1930. The Fauna of British India, including Ceylon and Burma. (Birds.) 8 vols. London: Taylor and Francis.

Bannerman, D. A.

1930–1951. The Birds of Tropical West Africa. 8 vols. London: Crown Agents for Colonies.

Bartsch, P.

1903. Notes on the herons of the District of Columbia. Smithson. Misc. Coll., 45: 104–111.

BEDDARD, F. E.

1898. The Structure and Classification of Birds. xx + 548 pp. London and New York: Longmans, Green and Co.

BEEBE, C. W.

1906. The Bird, its Form and Function. xii + 496 pp. New York.

1915. A *Tetrapteryx* stage in the ancestry of birds. Zoologica, 2:39–52.

1918–1922. A Monograph of the Pheasants. 4 vols. London: New York Zoological Society.

BEECHER, W. J.

1950. Convergent evolution in the American orioles. Wilson Bull., 62:51–86.

1951. Adaptations for food-getting in the American blackbirds. Auk, 68:411–440.

BOUBIER, M.

1925. L'évolution de l'ornithologie. ii + 307 pp. Paris: Felix Alcan.

BREHM, A. E.

1861. Das Leben der Vogel. xx + 707 pp. Glogau.

1864–1869. Illustrirtes Thierleben. 6 vols. Hildburghausen: Bibl. Inst.

BRUCH, C. F.

1828. Ornithologische Beiträge. Isis von Oken, 21:718–733.

1843. (Section für Zoologie, vierte Sitzung, am 23 September 1842) Deutsch. Naturf. Versamml. Ber., 1843:209–210.

BULLER, W. L.

1872–1873. A History of the Birds of New Zealand. xxiv + 384 pp. London.

BURT, W. H.

1930. Adaptive modifications in the woodpeckers. Univ. Calif. Publ. Zool., 32:455–524.

CHAPIN, J. P.

1932–1939. The Birds of the Belgian Congo. 2 vols. Bull. Amer. Mus. Nat. Hist., Nos. 65 and 75.

COLE, L. J.

1902. Suggestions for a method of studying the migrations of birds. Rept. Michigan Acad. Sci., 1902:67–70.

COOKE, W. W.

1888. Report on the Bird Migration in the Mississippi Valley in the Years 1884 and 1885. Bull. U. S. Bur. Biol. Surv., No. 2, 313 pp. Washington, D. C.

COPE, E. D.

1871. Synopsis of the extinct batrachia, reptilia and aves of North America. Trans. Amer. Philos. Soc., n.s., 14:1–252 + viii. Aves section, pp. 236–240.

1876. On a gigantic bird from the Eocene of New Mexico. Proc. Acad. Nat. Sci. Phila., 28:10–11.

CORY, C. B., C. E. HELLMAYR, and H. B. CONOVER

1918–1949. Catalogue of Birds of the Americas. Publ. Field Mus. Nat. Hist., Vol. 13, Pts. 1–11. (Publ. in 15 vols.)

COUES, E.

1872. Key to North American Birds. viii + 361 pp. Salem.

DAMES, W.

1884. Ueber *Archeopteryx*. Palaeont. Abhandl., 2:117–196.

Darwin, C.

1859. On the origin of species by means of natural selection. x + 502 pp. London: J. Murray.

Delacour, J.

1951. The Pheasants of the World. 347 pp. London: Country Life Ltd.

Dickey, D. R., and A. J. van Rossem

1938. The Birds of El Salvador. Field Mus. Nat. Hist. (Zool. Ser.), 23:1–635.

Dobzhansky, T.

1937. Genetics and the Origin of Species. xviii + 446 pp. New York: Columbia Univ. Press.

Dresser, H. E.

1871–1890. A history of the birds of Europe, including all species inhabiting the western palaearctic region. 9 volumes. London.

Drost, R.

1950. Study of bird migration 1938–1950. Proc. 10th Internat. Ornithol. Congr., 216–240.

Elliot, D. G.

1864–1865. A Monograph of the Tetraoninae: or, Family of the Grouse. xx + 52 pp., 27 col. pls. New York.

1870–1872. A Monograph of the Phasianidae or Family of the Pheasants. 2 vols. New York.

1877–1882. A Monograph of the Bucerotidae, or Family of the Hornbills. xxxii + (2) + 146 pp., 60 pls. (57 col.). London.

1895. North American Shore Birds, a History of the Snipes, Sandpipers, Plovers and Their Allies. . . . xvi + 17–268, 72 pls. New York.

Engels, W. L.

1940. Structural adaptations in thrashers (Mimidae: Genus *Toxostoma*) with comments on interspecific relationships. Univ. Calif. Publ. Zool., 42:341–400.

Farner, D. S.

1950. The annual stimulus for migration. Condor, 52:104–122.

Finsch, O.

1867–1868. Die Papagaien. 2 volumes. Leiden.

Finsch, O., and G. Hartlaub

1870. Die Vogel Ost-Afrikas. x + 897 pp. Leipzig.

Fisher, H. I.

1946. Adaptations and comparative anatomy of the locomotor apparatus of New World vultures. Amer. Midl. Nat., 35:545–727.

Friedmann, H.

1929. The Cowbirds. xvii + 421 pp. Springfield, Ill. and Baltimore, Md.: C. C. Thomas.

1948. The Parasitic Cuckoos of Africa. Wash. Acad. Sci. Monogr. No. 1. 204 pp.

Fürbringer, M.

1888. Untersuchungen zur Morphologie und Systematik der Vogel, zugleich ein Beitrag zur Anatomie der Stütz-und Bewegungsorgane. 2 vols. xlix + 1751 pp. Amsterdam: van Holkema.

Gadow, H. F.

1891. Vogel. *In* Bronn's Klassen und Ordnungen des Thier-Reichs, Vol. 6. 1008 pp. Leipzig: C. F. Winter.

Garrod, A. H.

1873a. On the carotid arteries of birds. Proc. Zool. Soc. London, 1873:147–472.

1873b. On certain muscles of the thigh in birds and their value in classification. Pt. I. Proc. Zool. Soc. London, 1873:626–644.

1874. On certain muscles of the thigh in birds and their value in classification. Pt. II. Proc. Zool. Soc. London, 1874:111–123.

Gatke, H.

1891. Die Vogelwarte Helgoland. xii + 609 pp. Braunschweig.

Glenny, F. H.

1940. A systematic study of the main arteries in the region of the heart. Aves. Anat. Rec., 76:371–380.

Gloger, B. von

1833. Das Abändern der Vögel durch Einfluss des Klima's. xxix + 159 pp. Breslau: Schulz and Co.

Gould, J.

1840–1848. The Birds of Australia. 7 vols., 600 col. pls. London.

1851–1869. (Suppl. to above.) iv + 158 pp., 81 col. pls. London.

1849–1861. A Monograph of the Trochilidae, or Family of Humming-Birds. 5 vols. London.

Grassé, P. P. *et al.*

1950. Oiseaux. Vol. 15 of Traité de Zoologie, Anatomie, Systematique, Biologie. 1164 pp. Paris: Masson et cie.

Groebbels, F.

1932–1937. Der Vogel. 2 vols. Berlin: Gebr. Borntraeger.

Harris, H.

1928. Robert Ridgway. Condor, 30:5–118.

Hartert, E.

1903–1923. Die Vögel der paläarktischen Fauna. 3 vols. Berlin and London.

Hartert, E., H. F. Witherby, F. C. R. Jourdain, and N. F. Ticehurst

1912. A Hand-List of British Birds, with an Account of the Distribution of Each Species in the British Isles and Abroad. xii + 237 pp. London.

Hartlaub, G.

1857. System der Ornithologie Westafrica's. lxvi + 280 pp. Bremen.

Heilmann, G.

1926. The Origin of Birds. vi + 208 pp. London: Witherby.

Heinroth, O.

1910. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. Verh. 5te. Ornithol. Kongr., pp. 589–702.

Heinroth, O., and M. Heinroth

1926–1928. Die Vögel Mitteleuropas. 3 vols. Berlin: Hugo Bermühler.

1941. Das Heimfinde-Vermögen der Brieftaube. Journ. Ornithol., 89:213–256.

Hellmayr, C. E.

1918–1949. [See Cory, C. B., C. E. Hellmayr, and H. B. Conover.]

Herrick, F. H.

1901. The Home Life of Wild Birds. xix + 148 pp. New York and London: Knickerbocker Press.

Hofer, H.

1949. Die Gaumenlücken der Vögel. Acta Zool. Internat. Tidskr. Zool., 30:209–248.

Homeyer, E. F. von

1881. Die Wanderungen der Vögel mit Rücksicht auf der Züge der Säugethiere, Fische und Insecten. 415 pp. Leipzig.

1885. Verzeichniss der Vögel Deutschlands. 16 pp. Vienna.

Howard, H. E.

1907–1915. The British Warblers. 2 vols. in 10 pts. London: R. H. Porter.

1920. Territory in Bird Life. vi + 308 pp. London: John Murray.

Howard, Hildegarde

1947. A preliminary survey of trends in avian evolution from Pleistocene to Recent time. Condor, 49:10–13.

1950. Fossil evidence of avian evolution. Ibis, 92:1–21.

Hudson, G. E.

1937. Studies on the muscles of the pelvic appendage in birds. Amer. Midl. Nat., 18:1–108.

1948. Studies on the muscles of the pelvic appendage in birds. 2: The heterogeneous order Falconiformes. Amer. Midl. Nat., 39:102–127.

Hudson, W. H.

1920. Birds of La Plata. 2 vols. London.

Huxley, T. H.

1867. On the classification of birds; and on the taxonomic value of the modifications of certain of the cranial bones observable in that class. Proc. Zool. Soc. London, 1867:415–472.

Ising, G.

1945. Die physikalische Möglichkeit eines tierischen Orientierungssinnes auf Basis der Erdrotation. Arckiv f. Matematik, Astron. och Fysik, Bd. 32A. No. 18. 23 pp.

Kessler, Karl F.

1853. Einige Beiträge zur Wanderunggeschicte der Zugvögel. Bull. Soc. Nat. Moscou, 26(1):166–204.

Kleinschmidt, O.

1900. Arten oder Formenkreise. Journ. f. Ornithol., 48:134–139.

1926. Die Formenkreislehre und das Weltwerden des Lebens. x + 188 pp. Halle.

1930. *Ibid.* Trans. into English as: The Formenkreis Theory and the Progress of the Organic World. London: H. F. and G. Witherby.

Knowlton, F. H.

1909. Birds of the World. xiii + 873 pp. New York.

Kramer, G.

1949. Über Richtungstendenzen bei der nächtlichen Zugenruhe gekäfigter Vögel. Ornithol. als Biol. Wiss., pp. 269–283. Heidelberg: Carl Winter.

1950. Eine neue Methode zur Erforschung der Zugorientierung und die bisher damit erzielten Ergenbnisse. Proc. 10th Internat. Ornithol. Congr., pp. 269–280.

Lack, D.

1939. The behaviour of the robin. Pts. I and II. Proc. Zool. Soc. London, 109 A:169–219.

Lambrecht, K.

1933. Handbuch der Palaeornithologie. xix + 1024 pp. Berlin: Gebr. Borntraeger.

Lorenz, K.

1931. Beiträge zur Ethologie sozialer Corviden. Journ. f. Ornithol., 79:67–120.

1935. Der Kumpan in der Umwelt des Vogels. Journ. f. Ornithol., 83:137–213, 289–413.

1937. The companion in the bird's world. Auk, 54:245–273.

Lowe, P. R.

1944. An analysis of the characters of *Archaeopteryx* and *Archaeornis*. Were they reptiles or birds? Ibis, 86:517–543 (figs. 5–10).

Marsh, O. C.

1870. Notice of some fossil birds, from the Cretaceous and Tertiary formations of the United States. Amer. Journ. Sci., ser. 2, 49:205–217.

1872. Preliminary description of *Hesperornis regalis*, with notices of four other new species of Cretaceous birds. Amer. Journ. Sci., ser. 3, 3:360–365.

1880. Odontornithes: A monograph on the extinct toothed birds of North America. Rept. Geol. Expl. 40th Parallel, pp. 1–201.

Mathews, G. M.

1910–1928. The Birds of Australia. 12 vols. London.

Mayr, E.

1935. Bernard Altum and the Territory theory. Proc. Linn. Soc. New York, 45–46: 24–38.

1942. Systematics and the Origin of Species. xiv + 334 pp. New York: Columbia Univ. Press.

1950. Speciation in birds. Progress report on the years 1938–1950. Proc. 10th Internat. Ornithol. Congr., pp. 91–131.

Mayr, E., and D. Amadon

1951. A Classification of Recent Birds. Amer. Mus. Nov., no. 1496, 42 pp.

Mayr, E., E. G. Linsley, and R. L. Usinger

1953. Methods and Principles of Systematic Zoology. vii + 328 pp. New York: McGraw-Hill.

McDowell, S.

1948. The bony palate of birds. Pt. I. The Palaeognathae. Auk, 65:520–549.

Mendel, G.

1865. Versuche über Pflanzen-Hybriden. Verh. Naturf. Ver. Brünn. Bd. 4.

Miller, A. H.

1937. Structural modifications in the Hawaiian goose (*Nesochen sandvicensis*) a study in adaptive evolution. Univ. Calif. Publ. Zool., 42:1–80.

1941. Speciation in the avian genus *Junco*. Univ. Calif. Publ. Zool., 44:173–434.

Miller, L. H.

1909. *Pavo californicus*, a fossil peacock from the Quaternary asphalt beds of Rancho La Brea. Univ. Calif. Publ. Dept. Geol., 5:439–448.

Miller, L. H., and Ida DeMay

1942. The fossil birds of California. Univ. Calif. Publ. Zool., 47:47–142.

Milne-Edwards, A.

1867–1871. Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France. Vol. I, 474 pp.; vol. II, 632 pp. Atlas, 200 pls. in 2 vols. Paris: Masson et cie.

MORGAN, C. LLOYD

1896. Habit and Instinct. 351 pp. New York and London: Edward Arnold.

MÜLLER, J. P.

1847. Nachtrag zu der Abhandlung über die Stimmorgane der Passerinen. Arch. Anat. Physiol., 1847:397–399.

MURPHY, R. C.

1936. Oceanic Birds of South America. 2 vols. Amer. Mus. Nat. Hist. New York.

NEWTON, A.

1893–1896. A Dictionary of Birds. 1088 pp. London.

NEWTON, E. T.

1886. On the remains of a gigantic species of bird (*Gastornis klaasseni*, n. sp.) from the Lower Eocene beds near Croydon. Trans. Zool. Soc., 12:143–160.

NICE, MARGARET M.

1937. Studies in the life history of the song sparrow. I. Trans. Linn. Soc. New York, 4:1–247.

1943. Studies in the life history of the song sparrow. II. Trans. Linn. Soc. New York, 6:1–328.

1941. The role of territory in bird life. Amer. Midl. Nat., 26:441–487.

NIETHAMMER, G.

1937–1942. Handbuch der Deutschen Vogelkunde. 3 vols. Leipzig: Akademische Verlagsgesellschaft M.B.H.

NOPCSA, F.

1907. Ideas on the origin of flight. Proc. Zool. Soc. London, 1907:223–236.

OATES, E. W., and W. T. BLANFORD

1889–1898. The Fauna of British India, including Ceylon and Burma. Birds. 4 vols. London.

ODUM, H. T.

1948. The bird navigation controversy. Auk, 65:584–597.

OLIVER, W. R. B.

1930. New Zealand birds. Wellington, N. Z.

OWEN, R.

1863. On the *Archeopteryx* of von Meyer, with a description of the fossil remains of the longtailed species from the lithographic stone of Solnhofen. Phil. Transact. London, 33–47.

1866–1868. On the Anatomy of Vertebrates. Vol. 2. viii + 592 pp. London: Longmans, Green and Co.

PALMÉN, J. A.

1876. Ueber die Zugstrassen der Vogel. 292 pp. 8 vols. Leipzig: W. Engelmann.

PETERS, J. L.

1931–1951. Check-list of Birds of the World. 7 vols. Cambridge, Mass.: Harvard Univ. Press.

PETRONIEVICS, B.

1921. Ueber das Becken, den Schultergürtel und einige andere Teile der Londoner *Archaeopteryx*. Genf., 1–31.

PHILLIPS, J. C.

1922–1926. A Natural History of the Ducks. 4 vols. Boston.

Pycraft, W. P.

1910. A History of Birds. 31 + 458 pp. London.

Reichenow, A.

1875. *In* "Protokoll der constituirenden Früjahrs-Versammlung." Journ. f. Ornithol., 23:347.

1893. System und Genealogie. Ornithol. Monatsber., 1:113–117.

Rensch, B.

1929. Das Prinzip geographischer Rassenkreise und das Problem der Artbildung. Berlin: Gebr. Borntraeger.

Richardson, F.

1942. Adaptive modifications for tree-trunk foraging in birds. Univ. Calif. Publ. Zool., 46:317–368.

Ridgway, R.

1869. Notices of certain obscurely known species of American birds. Proc. Acad. Nat. Sci. Phila., 21:125–135.

1881. Nomenclature of North American birds chiefly contained in the United States National Museum. Bull. U. S. Nat. Mus., 21:1–94.

Ridgway, R., and H. Friedmann

1901–1950. The Birds of North and Middle America. Bull. U. S. Nat. Mus., Vol. 50, pts. 1–11.

Rothschild, Miriam, and Teresa Clay

1952. Fleas, Flukes and Cuckoos. xiv + 304 pp. New York: Collins.

Rowan, W.

1931. The Riddle of Migration. xiv + 151 pp. Baltimore: Williams and Wilkins.

Rydzewski, W.

1950. Bird-Ringing Schemes Known to Be Operating at Present. Proc. Tenth Internat. Ornithol. Congr., pp. 356–359.

Salvin, O., and F. D. Godman

1879–1904. Biologia Centrali-Americana. Aves. 4 vols. London.

Saunders, H.

1889. An Illustrated Manual of British Birds. 40 + 754 pp. (1st ed.) London.

1899. An Illustrated Manual of British Birds. 40 + 776 pp. (rev. ed.) London.

Schlegel, H.

1828. Verhandeling ter Beantwoording der Vrage: "Daar er nog veel Duisterheid en Verschil van Gevoelens Platts heeft omtrent de Gewesten, waarheen zich de bij ons bekend gewordene Trekvogels begeven, etc." Vern. holl. Maat. Wet. Haarlem (2), 16:129–292.

1844a. (See Siebold, 1844.)

1844b. Kritische Uebersicht der Europäischen Vögel. 2 pts., pt. 1, 135 pp; pt. 2, 116 pp. Leiden and Paris.

Sclater, P. L., and W. H. Hudson

1888–1889. Argentine Ornithology. A Descriptive Catalogue of the Birds of the Argentine Republic. 2 vols. London.

Seebohm, H.

1887. The Geographical Distribution of the Family Charadriidae, or the Plovers, Sandpipers, Snipes, and Their Allies. xxix + 524 pp. London.

SELOUS, E.

1901. Bird Watching. xi + 347 pp. London.

1905a. Bird Life Glimpses. viii + 355 pp.

1905b. The Bird Watcher in the Shetlands. x + 388 pp.

SHARPE, R. B.

1899–1909. Hand-List of the Genera and Species of Birds in the British Museum. 5 vols. London.

SHARPE, R. B., and others

1874–1898. Catalogue of the Birds in the British Museum. 27 vols. London.

SHELLEY, G. E. (and, in part) W. L. SCLATER

1896–1912. The Birds of Africa, Comprising All Species Which Occur in the Ethiopian Region. 5 vols. 502 pp. London.

SHUFELDT, R. W.

1891. Fossil birds from the Equus beds of Oregon. Amer. Nat., 25:818–821.

SIEBOLD, PH. FR. DE

1844–1850. Fauna Japonica: Aves: Temminck, C. J., and Schlegel, H. Lugduni Batavorum, Apud A. Arnz et socios.

STEINER, H.

1917. Das Problem der Diastataxie des Vogelflügels. Jenaische Zeitschr. f. Naturwiss., 55:221–496.

STOLPE, M.

1932. Physiologisch-anatomische Untersuchungen über die hintere Extremität der Vögel. Journ. f. Ornithol., 80:161–247.

STRESEMANN, E.

1927–1934. Aves-Vögel. *In* Kükenthal und Krumbach, Handbuch der Zoologie, Bd. 7 (2te Hälfte). 899 pp., 944 figs. Berlin: De Gruyter.

1951. Die Entwicklung der Ornithologie. xv + 431 pp. Berlin: F. W. Peters.

STRONG, R. M.

1939–1946. A Bibliography of Birds. Field Mus. Nat. Hist. (Zool. Ser.), 25, pts. 1–3.

SWANN, H. K., and A. WETMORE

1924–1945. A Monograph of the Birds of Prey. London.

SWINTON, W. E.

1934. A Guide to the Fossil Birds, Reptiles and Amphibians in the Dept. Geol. and Palaeont. Brit. Mus. (Nat. Hist.). London.

THOMSON, J. A.

1923. The Biology of Birds. xi + 436 pp., 9 pls., 59 figs. London.

TINBERGEN, N.

1936. The problem of sexual fighting in birds; and the problem of the origin of "territory." Bird Banding, 7:1–8.

1939a. The behavior of the Snow Bunting in spring. Trans. Linn. Soc. New York, 5:1–95.

1939b. On the analysis of social organization among vertebrates, with special reference to birds. Amer. Midl. Nat., 21:210–234.

1942. An objective study of the innate behaviour of animals. Bibl. Biotheor., 1:39–98.

1948. Social releasers and the experimental method required for their study. Wilson Bull., 60:6–52.

1951. The Study of Instinct. xii + 228 pp. London: Oxford Univ. Press.

Tinbergen, N., and A. C. Perdeck

1950. On the stimulus situation releasing the begging response in the newly hatched Herring Gull chick (*Larus a. argentatus* Pont.). Behaviour, 3:1–38.

Watson, J. B., and K. F. Lashley

1915. An historical and experimental study of homing. Pap. Dept. Mar. Biol. Carnegie Inst., 7:9–83, 6 pls., 9 figs.

Wetmore, A.

1921. A fossil owl from the Bridger Eocene. Proc. Acad. Nat. Sci. Phila., 73:455–458.

1940. A check-list of the fossil birds of North America. Smithsonian Misc. Coll., 99 (no. 4):1–81.

1950. Presidential Address. Recent Additions to Our Knowledge of Prehistoric Birds 1933–1949. Proc. 10th Internat. Ornithol. Congr., 51–74.

White, G.

1789. The natural history of Selborne. v + 468 + (13). London.

Witherby, H. F., F. C. R. Jourdain, N. F. Ticehurst, and B. W. Tucker

1943. The Handbook of British Birds. (Rev. ed.). 5 vols. London: H. F. and G. Witherby.

Wolfson, A.

1945. The role of the pituitary, fat deposition, and body weight in bird migration. Condor, 47:95–127.

Wood, C.

1931. An Introduction to the Literature of Vertebrate Zoology. xix + 643 pp. London: Oxford Univ. Press.

Yarrell, W.

1837–1843. A History of British Birds. 3 vols. London.

Yeagley, H. L.

1947. A preliminary study of a physical basis of bird navigation. Journ. Applied Physics, 18:1035–1063.

Zimmer, J. T.

1931. Studies of Peruvian Birds. I. Amer. Mus. Nov., no. 500, pp. 1–23.

MAMMALOGY IN NORTH AMERICA

By W. J. HAMILTON, JR.
Cornell University

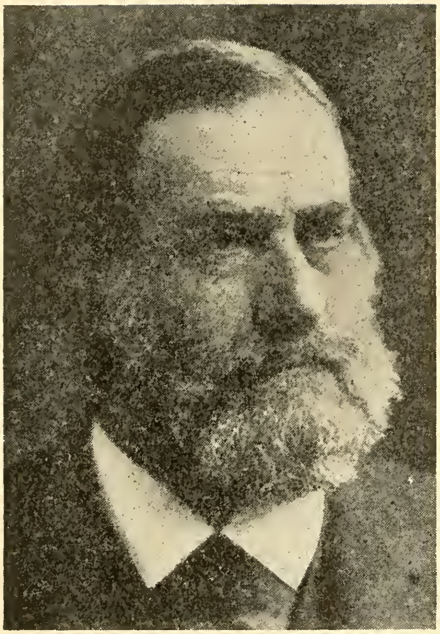
FROM THE DAWN OF HISTORY, mammals have played a vital part in the destiny of man. The mammal fauna of North America has been of tremendous economic significance, in one manner or another, to human populations. As food for the earlier settlers, many species provided, and continue to do so, a source of meat of not inconsiderable quantity. The peltries of our fur-bearers supply a substantial revenue to the trapper. Once the primary fur animal of the continent, the beaver influenced the exploration and settlement of the West and the northern latitudes. Esthetic values are not so tangible, but are evident in the hordes of tourists who annually visit our national parks to see the great bears and hoofed species as well as the attractions of the geysers, waterfalls, and other natural phenomena. On the other hand, the losses sustained through destruction of crops and foodstuffs by mammals may be very great. Some species play a major role in the transmission of disease organisms, such as sylvatic plague, murine typhus, spotted fever, rabies, and others of lesser importance. These economic relations have inspired extensive studies, through which much has been learned regarding the habits of certain species. The results of these investigations are continually being catalogued. Research in the field has not kept pace with that accomplished on some of the other classes of animals, for mammals are often shy and retiring in their habits and many are nocturnal, making observation difficult.

The study of mammals needs no economic justification, although pure research has been repeatedly applied to factors which relate to man's welfare. This has been aptly expressed by Miller (1928).

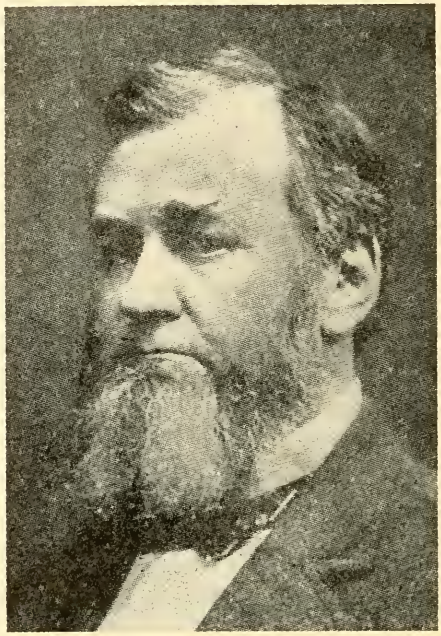
> There is nothing to be gained by denying that discovery for its own sake has always been the mainspring of work in all branches of scientific endeavor, including mammalogy. . . . This incentive requires no other apology than an indication of how the knowledge thus gained has contributed to human advancement. Indeed, an understanding of the relationships between the obscure seeker after facts and man's well-being must forever justify the worker in pure research.

The science of mammalogy may be said to date back only to the time of Linnaeus. Prior to the middle of the eighteenth century, the study of these animals had lacked conciseness. The binomial system of Linnaeus, however simple it may appear to present-day students, proved so useful a tool that it seems impossible that any serious study of animals or plants could have proceeded without it.

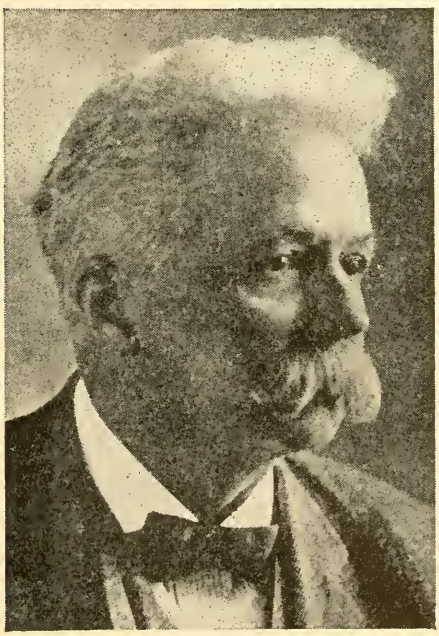
In his tenth edition of the *Systema Naturae,* published in 1758, Linnaeus included only 86 mammals. A century later, 220 kinds were known to North America alone. Presently, nearly 3,000 species and subspecies are recognized as occurring north of Panama. North of the Mexican boundary, nearly 400 full species are recognized today, some of these containing 40 subspecies alone. The number of



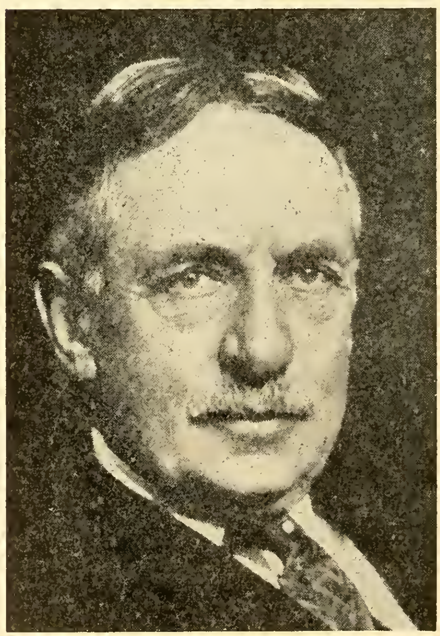
JOSEPH LEIDY
1823–1891



SPENCER FULLERTON BAIRD
1823–1887



CLINTON HART MERRIAM
1855–1942



HENRY FAIRFIELD OSBORN
1857–1935

fossil mammals that have been described almost equals that of living forms. It is presumed that when all the races are described, more than 20,000 will have been recorded from the entire world.

Few reference works were available to the early American biologists who had an interest in mammals. Richard Harlan, a close friend and supporter of Audubon, in 1825, published the first installment of his *Fauna Americana,* which treated mammals exclusively. While it was principally a compilation, based in large measure on Desmarest's *Mammalogie,* it served a useful purpose for the time. The following year John B. Godman's *North American Natural History, or Mastology,* lent further impetus to the study of mammals. There is much on the habits of the commoner species in this report. The first part of DeKay's *Zoology of New York,* dealing with the mammals, was published in 1842. This work includes considerable discussion of extra-limital species, and is a useful historical account.

For the first substantial report on the mammals of North America, we are indebted to Audubon and Bachman. The *Viviparous Quadrupeds of North America* appeared from 1846 to 1854. The plates, with a few exceptions, had been previously published in large oblong folio, without text, commencing as far back as 1840. The three volumes included 197 species, exclusive of varieties, of which about 160 were figured.

John Bachman has seldom been properly credited for his great contribution to American mammalogy. A lifetime spent in the ministry, he yet found time to make lasting contributions to science. His friendship with Audubon dated from 1831 until the latter's death twenty years later. Dr. Bachman was a learned zoologist of his day. In 1839, Audubon and he began work on the great *Quadrupeds.* Audubon was never to see the completed work, dying in 1851 when the first volume had been completed. His sons, John and Victor, were to color the plates and arrange for the editing and sales, but the greatest share would fall to Bachman, who was to make the dissections, write the systematic accounts and contribute largely to the text, through his vast knowledge of the life histories of the commoner species. Bachman had a restraining influence on his friend, cautioning Audubon repeatedly to exercise care in his spontaneity. In 1840, Bachman addressed his friend Audubon thus:

> When we meet, we shall talk about the partnership in the quadrupeds. I am willing to have my name stand with yours, if it will help the sale of the book. The expenses and the profits shall be yours or the boys. I am anxious to do something for the benefit of John and Victor, in addition to the treasures I have given them [Bachman was the father-in-law of Audubon's sons]. . . . Don't flatter yourself that the quadrupeds will be child's play. I have studied them all my life. We have much, both in Europe and America, to learn on this subject. The skulls and the teeth must be studied, and the color is as variable as the wind; down, down in the earth they grovel, while we, in digging and studying, may grow old and cross. Our work must be thorough. I would as soon stick my name to a *forged Bank Note* as to a mess of *Soupmaigre.*

Present-day students of mammalian life histories critically examine, or should do so, the pages of the *Quadrupeds* before commencing a serious study of any species. The difficulties of vertebrate research in the early nineteenth century, particularly the review of literature and access to museum specimens, are set forth in the introduction of the *Quadrupeds.* The young field naturalist will profit from reading this account.

Baird and the Smithsonian

At its inception, the Smithsonian Institution was charged with the responsibility for maintaining a museum. Spencer Fullerton Baird, then assistant to Secretary Henry submitted a report, detailing the need of research and publications that would accrue from such investigations. This was in accord with Henry's view.

The genius of Baird and his inspiration to the young collectors under him has not been fully appreciated. Baird had an enthusiasm and matchless knowledge of the vertebrates that will seldom be equaled. In 1853, Congress had appropriated $150,000 to defray the expenses of the survey of the various routes along which it was supposed that a railroad might be constructed from the Mississippi River to the Pacific. For this purpose, six parties were organized by the War Department. Through the efforts of Baird, persons capable of making collections and observations in natural history were assigned to these parties. These expeditions resulted in the most voluminous collections of the time. Earlier Wilkes (1838–1842) and his associates had made collections on the U. S. Exploring Expedition. Baird's study of these collections, particularly the mammals, was precise and stands as a monument to his untiring industry (Baird, 1857). While Baird presumably cared for the mammal collection until 1879, the U. S. National Museum was organized in that year by G. Brown Goode, under the instruction and guidance of Baird. Dr. Elliott Coues, distinguished ornithologist and mammalogist, was designated as curator of mammals. His *Fur-Bearing Animals*, a monograph of the North American Mustelidae published in 1877, was a classic of the time and is of lasting value. Frederick W. True, renowned for his studies on cetaceans, was curator of mammals from 1881 to 1908.

Gerrit S. Miller, Jr., is indelibly stamped in the minds of mammalogists for his *North American Recent Mammals* (Miller, 1924), the only check list of North American mammals presently available to the student. In this report synonomy, type locality, and distribution are given. While now an outdated reference work, it is still of considerable value to the student.

Remington Kellogg became curator of mammals upon Miller's retirement. His knowledge of vertebrates is unsurpassed. He has published in many fields, but his greatest contributions have been on cetaceans. Kellogg's place as a master zoologist was recognized in 1948 when he was made director of the U. S. National Museum. For a fuller account of the Smithsonian, the reader is referred to Kellogg (1946).

The Influence of Merriam on American Mammalogy

Clinton Hart Merriam had a profound effect upon mammalogy, indeed he was preeminent in the field. His accomplishments and influence on others will long be felt in American zoology. As a youngster in upstate New York, his passion for birds and mammals resulted in substantial early reports. Upon the completion of his medical school studies in 1879, Dr. Merriam practiced for six years in Locust Grove, but his growing interest in mammals was evident during this period. In 1884 his *Mammals of the Adirondaks* was published. This report set a new standard, embodying for the first time details of life histories that have seldom been surpassed in a local work. A year earlier he had begun correspondence with young Vernon Bailey, a Minnesota farm boy. This lad, later to become Merriam's brother-in-law, was an indefatigable collector. Through Bailey's well prepared specimens and large series of the less common species (at least in collections), Merriam may have been first encouraged to consider the possibility of a country-wide survey of mammals.

As with so many naturalists, Merriam's first love was ornithology. The founding of the American Ornithologists' Union in 1883 brought him in contact with the masters of the day, including Baird, Bendire, J. A. Allen, Ridgway, and others. He was elected secretary of the society. In 1885, through the efforts of the A.O.U., Congress authorized the establishment of a section of ornithology to be a branch of the Division of Entomology, then under the Commissioner of Agriculture. Merriam was appointed as ornithologist in this newly created section. He gave up the practice of medicine and assumed the duties that were to play so important a part in North American mammalogy. His fellow student in medical school, Dr. A. K. Fisher, was invited as assistant ornithologist. Most of us remember Fisher best for his *Hawks and Owls of the United States,* published in 1893. Within three years, the section became the Division of Economic Ornithology and Mammalogy. In 1905, the Bureau of Biological Survey was founded, an outgrowth of the smaller unit. We now know this bureau as the Fish and Wildlife Service, under the Department of the Interior.

Merriam assembled a group of able men for the Bureau, and sent collectors into the unexplored West. He inaugurated the technical North American Fauna series, revisions and description of mammals occupying many of these important publications. By the early 'nineties, Merriam had planned his life work; studies that would determine some of the factors which limit the distribution of plants, birds, and mammals. His descriptions of new mammals, including several distinctive genera, may be partially credited to the industry of Bailey, who was sending to Washington scores of undescribed forms.

The San Francisco Mountains of Arizona offered a splendid opportunity to study altitudinal distribution. The report of this trip gave a clue to his later reports on distribution (Merriam and Stejneger, 1890). However modified in later years, the Arizona study was fundamental. Many may disagree with his temperature laws, but in parts of North America these have stood the test of time. To be sure, there are valid objections to these "temperature summations," but they appear to hold in a great part of western North America.

The standards of Merriam were of the highest caliber. However harsh he might appear to some, he gave freely of advice and aided many an aspiring youngster. Recently I have seen his entire correspondence to one of his field assistants, a collector of no mean ability. When this assistant offered to resign, feeling that he had been accused of misusing government property, Merriam wrote in longhand, on plain paper, the following letter, dated June 14, 1894.

Don't lose your head, even if the provocation seems great—from your standpoint. It is evident that I was mistaken as to what you actually did. I thought you had sawed up or made a packing box of the two trays from the *new* chest we sent you last—not dreaming that you had kept two trays of the old chest with you so long.

Please bear in mind that I am held *personally responsible* to the Department for all property belonging to the Division, and am now charged with several hundred dollars worth of property that has gone in the field and not likely to be returned.

The most important single thing for a young man to learn is *self control*—without this he cannot hope to fill a useful field among his fellow men. If you ever get so very mad you feel you must write an impudent letter, the best way is to sit right down and write it and say all the mean things you can think of. Then take the letter and your hat, having relieved your mind, and take a walk to some secluded spot. Then take out your match box and set fire to the letter and stay by it until it has been decomposed into its chemical constituents. Whatever you do, don't ever mail such a letter—particularly in an official capacity.

Furthermore, don't mix personal and official matters in the same letter. Always write as freely as you wish about personal things, only not on the same sheet with your official letters which go on file.—C. H. M.

The influence of Merriam on younger naturalists of the time cannot be denied. His greatest student was Vernon Bailey, a heroic figure in American mammalogy. Many "unknowns," later to become celebrated for their own researches, collected for him. E. W. Nelson, E. A. Goldman, and W. H. Osgood may be numbered among his illustrious "students." Dr. Nelson later served as chief of the Biological Survey (1916–1927), Goldman is noted for his Mexican surveys, and Wilfred H. Osgood was director of zoology at the Chicago Natural History Museum at the time of his death. For a detailed account of Merriam, the reader should see the stimulating account by Osgood (1943). Nearly 500 publications, many of monographic scope, are listed by Grinnell (1943).

The United States Biological Survey

No other organization has played such an outstanding role in American wildlife as has the U. S. Biological Survey. Its function is the investigation of life histories, habitats, ranges, distribution, and the economic, recreational, cultural, and other values of American birds and mammals. Over the years, a major emphasis has been placed on the repression of noxious rodents and predatory mammals where such was needed. The vast number of scientific publications detailing the researches conducted by this agency is without parallel.

When the first appropriation for a Branch of Economic Ornithology in the Division of Entomology was made in 1885, Americans were at long last becoming conscious of the increasing plight of our wildlife resources. They had seen the fate of the buffalo determined with completion of the Union Pacific. Ribbons of steel had separated the great beasts into a northern and southern herd, and the railroad provided the needed transport for the spoils of the hide hunters. Unwise introductions of exotics and the scandalous slaughter of wildlife had the effect of focusing attention on the plight of this great natural heritage. In its second year, the division took cognizance of mammals, primarily in their relation to agriculture and horticulture. It appears that Dr. Merriam had little use for the term "economic," and his leadership led to a steady subordination of the practical problems to those of the scientific. It was not long before his interests prevailed. Studies in geographic distribution, which Merriam considered equally or more important than the economic, took precedence over the practical. Economic and agricultural publications were to be published in the form of special reports or circulars (the familiar *Farmers' Bulletin*), while the scientific was to be brought out in the North American Fauna series. From 1891 until 1906, geographic distribution was the keynote of research, with economic relations playing a lesser role. This trend was reflected in the Secretary of Agriculture's report for 1890, in which he declared:

The name of this Division is unfortunate as it conveys an erroneous idea of the nature of its work. The division is in effect a biological survey, and should be so named, for its principal occupation is the preparation of large-scale maps of North America, showing the boundaries of the different faunas and floras, or life areas.

The results of these explorations bore fruit in 1894, when the divisional report for that year announced that the problem of temperature control of the geographic distribution of animals and plants had been solved. The Weather Bureau had provided temperature data which, when plotted on the biogeographic maps, conformed with a high degree of exactness to the boundaries of the life zones as established by Merriam.

For a decade, the biological exploration of North America continued. The geographic distribution of species in the West received major attention until 1906, when the Bureau of Biological Survey, as it was now called, again shifted its emphasis to economic problems. Merriam had selected his staff with care. His counsel and training of the young field agents did not go unrewarded. To one of his younger field naturalists, J. Alden Loring, Merriam wrote more than a score of letters in a matter of eight months. These are replete with instructions, criticism of skins, and helpful advice. It is presumed he carried on as lively a correspondence with his other field assistants. When he was not in the field, Merriam found time to initiate the Fauna series. From 1889 to 1896, this indefatigable scientist authored the first eleven of the fanual series, all of monographic scope. These were the first revisions and serious taxonomic studies ever made on North American mammals. They stand as a monument to Merriam's industry and taxonomic judgment. The advance of mammalogy at this time was fortunately not dependent on the resources of the government. In 1899, Edward H. Harriman organized and financed an expedition to Alaska, members of the Biological Survey sharing in the investigation. In succeeding years, the scope was enlarged to include Canada and Mexico.

In 1907, Congressional hearings resulted in partial abandonment of the distributional studies. More emphasis was expended on practical pursuits. The well known reports of Professor David E. Lantz now appear. Many of these are concerned with injurious rodents and measures for their control.

The undercurrent of public opinion that dictated this shift to a practical point of view was a sound one. With the amazing growth of agriculture and the consequent increase in the value of its products, information was sorely needed on the control of the many pests which took a huge annual toll. The agriculturist was no longer content with reports detailing the habits, distribution, and characters of the pests which pilfered his crops or destroyed his livestock. A new supply of food was available to the wolves and coyotes, and the stockmen took the brunt of this toll. An investigation of the wolf in relation to stock raising was published by Bailey (1907). This was followed by a shorter article by the same author, in which emphasis was placed on den hunting, with the subsequent destruction of the litter. Following the recommendations outlined in these reports, an estimated 1,800 wolves and 23,000 coyotes were accounted for in a single year. Not until 1915, with increasing depredation from predatory animals, did Congress relieve the Forest Service of this effort. With a sizable appropriation to the Survey, Congress directly ordered the destruction of "wolves, coyotes and other animals injurious to agriculture and animal husbandry on the national forests and the public domain," thus placing the responsibility directly on the Survey. This action may have been precipitated by a disastrous outbreak of rabies among wild animals in the West. In 1916 more than half of the appropriation for food habits research was expended in activities to control the wolf and coyote. Efforts to eradicate these animals have been continued.

Where conditions are suitable, poison is by far the most economical and efficient known agent for the destruction of the coyote, other predatory mammals, and rodents, where they are abundant. The continued use of this method in eradicating noxious species brought many objections. Many useful species were unintentionally killed. Valuable fur-bearers have been destroyed in considerable numbers. Continued protests by those who favored a reduction in poisoning operations and a modified policy of control by a government agency culminated in open discussion of the pros and cons of the method. A symposium on predatory animal control was held in New York City, May 21, 1930, at which scientists of the Biological Survey defended the program, while those from universities, museums, and other organizations brought out the dangers attendant on the widespread use of poison. For details of these discussions, the reader is referred to the August, 1930, issue of the *Journal of Mammalogy.*

The shift of emphasis from surveys and distributional studies to that of control of noxious pests was inevitable. Pressure from agriculture and livestock interests had brought this to pass. Without the purely scientific studies of the Merriam era, however, the distribution of various small mammals of economic significance would not have been known. When the call came for control, immediate steps could be taken and widespread efforts made at reduction. This is essential in controlling many of our western ground squirrels, for piecemeal efforts result only in temporary relief.

Other divisions of the survey have been occupied with mammal investigations. This is reflected in the scope of the reports that have been published in recent years. Until rather recently, the Division of Food Habits Research, while emphasizing the economic status of birds, had made marked contributions to our knowledge of wild mammal dietary. Such studies are essential in determining, in part, economic relationships. Considerable effort has been directed to the investigations and life histories of rodents, by far the major share of such studies being focused on the Norway rat. This unmitigated pest has no redeeming quality. The loss it occasions yearly to our foodstuffs and as an agent in the spread of disease is all too well known. Research directed toward new raticides has played a not inconsiderable part in our increasing and successful war against this arch enemy of man.

Research on fur-bearers, with special emphasis on problems of the fur farmer, has long been under the Division of Fur Resources. These investigations are concerned primarily with nutritional and disease studies.

The Federal Aid in Wildlife Restoration program was inaugurated in 1938 under the Pittman-Robertson Act, which provides for the use, in behalf of wildlife, of income from the Federal excise tax on sporting arms and ammunition. In the thirteenth year of the program, closing on June 30, 1951, a sum of $17,846,423 was made available for this work. Federal allotment is matched by a 25 per cent contribution from the states to carry out approved projects. Many of the state conservation departments and the state colleges and universities have profited by the funds thus made available for research. In a recent year, 184 individual projects were under way in 44 states, Alaska, Hawaii, Puerto Ricó, and the Virgin Islands, with emphasis on game and fur animals. In 1951, 33 states had research projects on deer, 22 were investigating fur-bearer problems, chiefly muskrat and beaver, while 11 were investigating rabbits and hares. Other mammals that have received attention are antelopes, squirrels, mountain sheep and goats, elk, moose, and bison. One of the most detailed state mammal surveys yet undertaken has been supported by Pittman-Robertson funds. This Pennsylvania project, under the direction of J. K. Doutt of the Carnegie Museum, has provided more details regarding the distribution and habits of the mammals inhabiting a single commonwealth than any previous study.

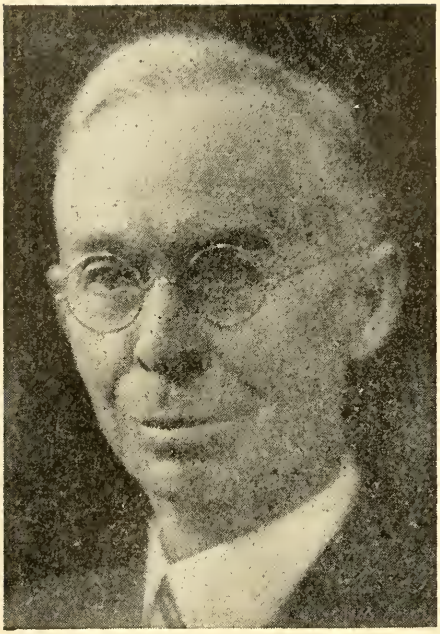
Under provisions of President F. D. Roosevelt's reorganization plan, made effective June 30, 1940, the Bureau of Fisheries and the Bureau of Biological Survey, in the Department of the Interior, with their respective functions, were consolidated into one agency, to be known as the Fish and Wildlife Service.

Progress in Paleontological Research

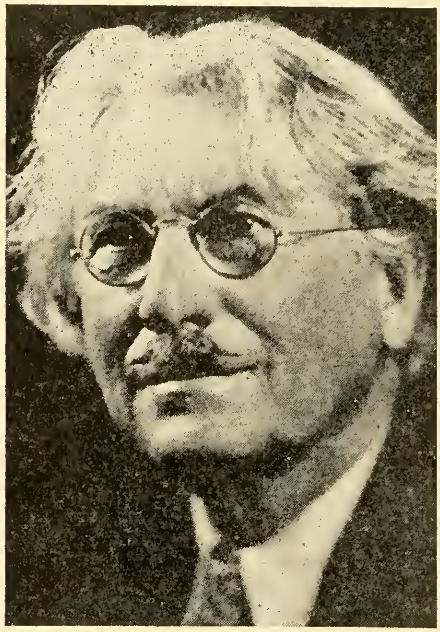
Few areas are so rich in fossil mammals as western North America. The successive assemblages of animals which once lived in this vast area have been faithfully studied for the past ninety years. John Evans, assistant to Dr. David D. Owen, Dr. F. V. Hayden of the U. S. Geological Survey, and others led important expeditions into this unexplored region. Collecting was not the prosaic occupation of today. Pack horses and wagons carried out the rewards of these expeditions to the single transcontinental railroad; hostile Indians made these explorations extremely hazardous.

Joseph Leidy was to lay the foundation for the science of American paleontology. Trained in medicine, Dr. Leidy had little time to devote to practice, the consuming interest in fossils occupying ever more of his efforts. Baird was instrumental in bringing to Leidy's Philadelphia laboratory the fruits of the Government survey collections. For many years Leidy, unable to accompany the western expeditions, was fully occupied with the fossils, which were never lacking in abundance. He was the American pioneer in paleontological research, describing the extinct oreodonts, camels, rhinoceroses, and titanotheres that roamed the Miocene. His more than two hundred papers on paleontological subjects culminated in a great work on the extinct mammalian fauna of Nebraska and Dakota (Leidy, 1869). This report includes a synopsis of the mammalian remains of North America. A fitting epitaph to this quiet and retiring scientist was given by Osborn, who praised him "as the last great naturalist in the world of the old type, who was able by both his capacity and training to cover the whole field of nature."

Marsh and Cope completed the triumvirate of the early paleontologists, following in the footsteps of Leidy. Independently wealthy, Marsh could muster his own expeditions. His graduate students at Yale accompanied the bone hunter on repeated expeditions to Colorado, Nebraska, Utah and Wyoming. Museums today display Marsh's prized collections of fossil horses, so valuable as a demonstration of evolution. These discoveries were among the finest of those made by Marsh.

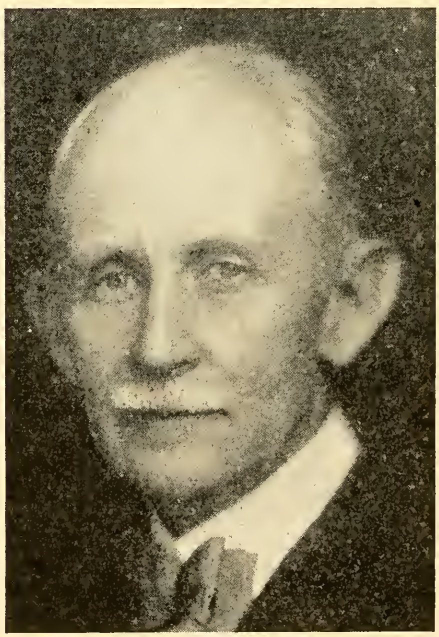


VERNON BAILEY
1864–1942



ERNEST THOMPSON SETON
1860–1947

RUDOLPH MARTIN ANDERSON
1876–



GERRIT S. MILLER, JR.
1869–

His ability as a field collector is reflected in the vast assemblage of mammalian fossils housed in Yale's Peabody Museum.

A student of Leidy, Edward Drinker Cope continued the study of fossils. As a youngster, his first love was the reptiles, and the young naturalist made lasting contributions to our knowledge of salamanders and lizards. His major contributions were made west of the Mississippi, while Cope was employed as vertebrate paleontologist of the U. S. Geological and Geographical Survey of the Territories. The contributions Cope made on the creodonts, canids, and felids were outstanding. His thousand-page volume on the vertebrates of the Tertiary Formations of the West includes accounts of 350 species, 90 percent of which the author had described (Cope, 1884).

The collecting of fossil remains is a slow and tedious process. Yet even greater effort must be employed in the museum when reconstructing the fruits of expeditions. Following the period of western exploration, the study of collections consisted in establishing the lineage of the families, orders, and classes. Many groups have been collected which provide a panoramic view of lineal descent. Among paleontologists of the present century, Henry Fairfield Osborn must receive special recognition. He was a rare combination of scientist, teacher, and administrator. From 1877, when he commenced paleontological research at Princeton, until his death in 1935, Professor Osborn published nearly a thousand articles and memoirs. Among his best known works are *The Age of Mammals* (1910), *Men of the Old Stone Age* (1916) and *The Titanotheres of Ancient Wyoming, Dakota and Nebraska* (1929). He somehow found time to write many popular articles and books, detailing the lives of creatures that lived in the past.

A Princeton classmate of Osborn, William B. Scott, contributed materially to the study of early mammals. His *History of Land Mammals in the Western Hemisphere* (1913), while designed primarily for lay readers, is of considerable service to the professional mammalogist.

It is difficult to single out individuals who have made lasting contributions in any field of science without creating injustices. The names of Edwin H. Colbert, William K. Gregory, Claude W. Hibbard, Remington Kellogg, William D. Matthew, John C. Merriam, George G. Simpson, Ruben A. Stirton, Chester Stock, Horace E. Wood, 2nd, and Jacob L. Wortman merit especial notice for their substantial reports on fossil mammals. Of these, Simpson has made particularly noteworthy contributions in recent years.

The Growth of Literature on Mammals

With the development of mammalogy in North America, it was apparent that many works would appear dealing with this group. Mention has been made of the *Quadrupeds of North America.* This stellar contribution was a model for its time. Even today, serious students of mammal habits consult the three volumes, for there is a wealth of information that is remarkable for the years in which they appeared. It is probable that if the authors had used a model life history outline, as we know of such today, their immense background of knowledge would have resulted in an even more lasting contribution. Audubon and Bachman did less credit to themselves and the animals they discussed than they might otherwise have done. The *Quadrupeds* is, nevertheless, an enduring monument to these two men.

Robert Kennicott, dead in the Arctic at thirty years, was a disciple of Baird. When only twenty-two years of age, he published a report on the mammals of Illinois, which includes substantial information on many common species (Kennicott, 1858).

The monumental Pacific Railroad report of Baird, who knew only 220 living kinds of North American mammals, was, in some respects, a standard until the time of Merriam. Between the two decades that separated the productive efforts of these two men, an amazing book appeared. In 1876, when only twenty-five years old, David Starr Jordan, then a young teacher in Wisconsin, published his *A Manual of the Vertebrates of Eastern United States.* It was, and still is, widely used, although now out of print. Jordan's *Manual* was the bible of many an early naturalist, for it included simple keys and brief descriptions of all of the known vertebrates occurring from the Atlantic coast to Iowa and south to North Caroline. Primarily an ichthyologist, Jordan had received a good basic training in the vertebrates at Cornell University.

The unparalleled publications of Merriam had set the style in the latter part of the nineteenth century. His *Mammals of the Adirondaks,* published in book form in 1884, remains a classic and a model for studies yet to come. We must not disregard the influence of Trouessart, whose *Catalogue Mammalium* (1897–1905) is a concise review of the then known mammals of the world.

During the next decade the important American publications on mammals were largely confined to the reports of the Biological Survey. The North American Fauna series appeared regularly, containing much on the systematics of our native species.

To detail the many excellent reports on mammals that have made their appearance in the past twenty-five years would be tiresome to the reader and serve no useful purpose. With what one writer might consider the highlights of achievement in the field of literature, a score stand ready to disagree. Subject matter and the major references will be listed, if only to give an index to the breadth of the subject. The inquisitive reader will find, in the documentations of the studies referred to below, the more important references that attempt to cover the subject.

General reference works on mammals are notable for their paucity. Flower and Lydekker's *Mammals Living and Extinct,* published in 1891, and Beddard's classic *Mammalia* in the Cambridge Natural History Series are inclusive accounts of the mammals of the world. Surely these volumes, together with Weber's *Die Saugetiere,* appearing in 1904, may be considered outstanding. The excellent but smaller volumes of Angel Cabrera *Manual de Mastozoologia* and Dr. F. Bourliere's *Vie et Moeurs des Mammifères* stress the ecological approach.

E. W. Nelson's popular account of North American mammals had a salutary effect on the study of our native species. Published by the National Geographic Society in 1916 and 1918, this report was embellished by the peerleess artistry of Louis Agassiz Fuertes. A decade before the appearance of these studies, the more serious student of mammalogy was treated to W. D. Scott's *History of Land Mammals in the Western Hemisphere.*

In 1929, Ernest Thompson Seton's *Lives of Game Animals* appeared. In his final words of the preface, he says:

. . . I do not consider that I am offering even a fragmentary presentation of the final truth that is coming. This I feel—that I am merely assembling tools, and some day a great man will come, and with these tools construct a telescope that shall surely reveal to us the vision that the world is awaiting.

Those of us who acknowledge Seton's gift for writing, his industry, and his impressive stature as a field naturalist will not long forget his zeal and ambitions. His ability to portray the animals as he saw them has seldom been surpassed. Seton's final effort, indeed his life work, was directed to the *Lives of Game Animals,* abetted by President T. R. Roosevelt. In this fine study, the value of which will long be felt, Seton made his greatest contribution in a singular manner. He liberally quotes the sources unavailable to many of the present generation. Well documented, the volumes indicate the sources he searched so assiduously, such as *Forest and Stream,* the published journals of the older naturalists, and other reports that are often hard to come by. Diligent search in any sizable library will find the old notes but Seton brought them together. While one may read a dozen pages without learning much that is new, the fascinating manner in which Seton put them down will long be remembered.

Many who read Seton's account of a species consider that what he did not record *must* be new. On the contrary, one can read pages without end in the *Lives* and find that the study of any one species is yet undeveloped. Seton's volumes on the game animals are a beginning. He amassed the data that have helped us all, but the work is an unfinished report, as Seton knew.

More recently, the *Mammals of North America* by Victor Cahalane has provided a wealth of information. His lucid accounts are detailed and provide a ready source of information on our native species. The volumes by Francis Harper *Extinct and Vanishing Mammals of the Old World* and the late Glover M. Allen's *Extinct and Vanishing Mammals of the Western Hemisphere,* published in 1945 and 1942 respectively by the American Committee for International Wildlife Protection, are models of inclusive but concise reports, so thoroughly documented that any biologist can ill afford to pass them by without study.

The *American Midland Naturalist, Ecology,* and *Ecological Monographs, Journal of Wildlife Management,* the several Wistar Institute journals, and the publications of the state colleges and universities are rich in mammal lore. The many state academies have reports that are of interest to the mammalogist.

The result of the monumental effort of Gerrit S. Miller, Jr., in compiling the *List of North American Recent Mammals,* appeared in 1924. This indeed was the crowning effort to a lifetime of research. Included are synonyms, type localities, and usually the range of all the known mammals inhabiting the area from Panama to Greenland. A revision of this important work is in press, Dr. Remington Kellogg assisting Miller in the task.

A more recent check list is that of Anderson (1946). In his account of Canadian recent mammals, Dr. R. M. Anderson, dean of Canadian mammalogists, compiled a lifetime study of the mammals in the provinces north of our border. His knowledge of Canadian mammals is evident in this report.

The biology of any animal revolves, of necessity, around two major points. It must eat to live and, second, it must reproduce to perpetuate its kind. The comprehensive story of reproduction is brought fully to date by Asdell's *Patterns of Mammalian Reproduction,* published in 1946, in which the author collated most of the data bearing on the reproductive behavior of wild as well as domestic mammals.

An excellent summary of the economic relations of mammals has been compiled by Henderson and Craig (1932). This book includes a wealth of data on the practical aspects of mammals, particularly as related to man. The references on the dietary of wild mammals are quite complete. The volume is thoroughly documented.

Probably more people have been attracted to the many fields of natural history by pocket guides than from any other source. Mammal books have not kept pace with allied fields in this respect. Bird guides, and good ones too, are without end; we have pocket editions of books that are aids in determining plants, insects, shells, and the like. A handy guide for the identification of mammals is another matter. Many species have subtle differences which are hard to see, let alone differentiate. Anthony's *Field Book of North American Mammals,* published in 1928, established the amateur's interest in mammals. Covering all of North America, Anthony included descriptions of species and their races, some maps indicating present known ranges, and some figures that were considered helpful for identification. It is a valued contribution to mammalogy. As this report is being written, yet another small book appears. *A Field Guide to the Mammals,* by W. H. Burt and Richard Grossenheider, is a specific example of the trend in American natural history. A splendid book, embellished with no end of colored plates, maps, and figures of tracks, it will serve as a model for years to come. Pocket books on natural history have undoubtedly brought many amateurs into specific fields of study, and many of these naturalists have made substantial contributions to our knowledge.

Animals are no respecters of political boundaries. Yet the dictates of man all too often indicate that faunal surveys shall be made within a single state or province. Hence political lines, rather than natural boundaries, often limit the reports of these faunal studies. Many state reports on mammals have appeared. Among these, special mention must be made of Lyons' *Mammals of Indiana,* Vernon Bailey's *Mammals of New Mexico* and *The Mammals and Life Zones of Oregon,* W. B. Davis's *The Recent Mammals of Idaho,* Burt's *Mammals of Michigan,* E. R. Hall's *Mammals of Nevada,* Dalquest's *Mammals of Washington* and the comprehensive two-volume *Fur-Bearing Mammals of California,* by Grinnell, Dixon, and Linsdale. The account of a smaller region of a state, embracing a natural unit, is that of Harper (1927). This model report is one of the best local studies that has yet appeared.

An excellent summary of the development of the classification of mammals from Aristotle to Weber has been recorded by Gregory (1910). Simpson (1945) adequately summarizes the works that have influenced the development of mammalian classification.

Some universities fortunately have their own publications and can thus provide an outlet for substantial reports. Among these several institutions, most notable are the University of California Publications in Zoology, the University of Michigan's Miscellaneous Publications in Zoology and the University of Kansas publications.

The *Wildlife Review,* a mimeographed bulletin designed for the abstraction of articles bearing on wildlife management, first appeared in September, 1935.

It has served a real need of the legion engaged in this field. In the 73 issues that have appeared to date much mammal research has been summarized. The review is far more inclusive than the title indicates.

The American Wildlife Institute has sponsored reports of monographic scope on wolves, coyotes, and the puma. We may soon look for a treatise on deer.

The Growth of Mammal Collections

Early collections of mammals in the state cabinets and lyceums of natural history were notable only for their paucity. A century ago, the larger of these were owned by private collectors. With the growth of the large museums, many of the private collections were donated, sold, or bequeathed to the museums. In earlier days, most were displayed as mounted specimens, and emphasis was given the larger or more striking species. Since the primary function of a great museum is to promote research, it is apparent that large collections of the many species in a convenient form for study must be available to the specialist. For every mounted specimen in the showcases of the larger museums, usually more than a score and often hundreds are housed in the mammal collections reserved for study.

Figure 1. The cyclone trap, and its later refinement into the snapback trap as we know it today, made modern mammalogy possible. A few dollars provides the collector with sufficient traps to make a survey of any region possible. The smaller trap has taken a *Zapus*, while the Museum Special holds a *Condylura*. Few inventions have been so instrumental in furthering the growth and promotion of a specialized field in natural history.

We have seen the revolutionary change brought about by the invention of the snap-back trap. This little device, designed to take the smaller species, was responsible, within a few years after its appearance, for the hundredfold increase in the size of mammal collections.

The mammal collection of the Fish and Wildlife Service (more familiarly known as the Biological Survey) is limited to recent North and Middle America species, of which it has the largest representation of any collection in the world. Included in this great collection is the type of the smallest North American mammal, *Microsorex hoyi winnemana,* a tiny shrew weighing less than a dime. This elfin creature was collected by Edward A. Preble on the Potomac shoreline, almost within sight of the building where it is now housed. The collection also includes the type of the largest of all existing carnivores, *Ursus middendorfi,* collected on Kodiak Island, Alaska. Of the valued types, the survey collections contain 1,313, nearly half of the species and subspecies of North American mammals that are known today. These collections, like others, are indispensable in connection with the administration of wildlife, and are the basis for distributional, taxonomic, and identification studies. On June 30, 1952, this collection contained 146,237 catalogued specimens.

The United States National Museum collection contains mammals from all parts of the world. In recent years, about 2,000 specimens have been added annually. This collection now (1952) has 110,824 specimens. Major collections have been received in the past ten years from Alaska, the Canadian Arctic, Labrador, Costa Rica, Panama, and Colombia in the New World, and from Egypt, Sudan, Japan, Korea, Formosa, Philippines, Burma, Nepal, Siam, Borneo, Australia, and nearly all the island groups of the Pacific.

The American Museum of Natural History mammal collections contain more than 130,000 specimens. The many expeditions to South America, Asia, Africa, Madagascar, Australia, and Oceania have resulted in the discovery of many new species. Well over 800 types are represented in the museum. More than half of the collection is composed of North American specimens. In 1940, the Museum of Vertebrate Zoology, University of California, had in its collections slightly more than 100,000 skins. These were primarily representatives of the Pacific Coast, from Alaska to Lower California, the Great Basin, northern Mexico, and Salvador. This is a remarkably large collection for a university museum, more than twice the number contained in the University of Michigan, which may be considered the second largest mammal collection owned by an educational institution.

The increasing interest in mammals is reflected in the ever growing collections, both private and public. A survey of the existing North American collections was made by A. B. Howell in 1923. A comparison of the survey made by Doutt *et al.* (1945) and Howell's earlier study reveals many interesting changes in the twenty-year span. In this short period the number of specimens in collections more than doubled. The number of private collections had increased two and a half times, while public collections were almost five times as common as in 1923. Doutt's report lists 939,483 specimens in United States and Canadian collections, whereas only 410,239 specimens were recorded by Howell in 1923. Since 1943 even greater strides have been made. The National Museum collection is increasing by 2,000 specimens a year, while more than 8,000 specimens were added to the Biological Survey collections in the past nine years. The University of Michigan collections have increased correspondingly, approximately 10,000 specimens being added since Doutt's survey in 1943. Smaller collections have increased accordingly. The mammal collection at Cornell University has doubled in the past nine years. It is quite likely that other museums have added materially to their collections in the past decade.

The Conservation of Mammals

Early historians have left us with a record of the abundance of native mammals a century ago. The once widespread distribution of the big game species and their incredible numbers, even into the latter part of the nineteenth century, has been faithfully catalogued. The primitive population of the bison has been placed as high as 60,000,000, a figure which is probably extravagant. The pronghorned antelope, native only to western North America and typically a resident of the Great Plains, probably rivaled the bison multitudes. In the middle of the last century, the lordly American elk or wapiti roamed through eastern forests from Quebec to Georgia. The whaling industry flourished, bringing riches to the adventurous sea captains and their hardy crews. The pelts of fur animals were much in demand, prompting hardy trappers and traders to invade the uncharted wilderness in quest of a harvest. Many eastern towns, rivers, and lakes have taken their names from the beaver, substantial evidence of its widespread distribution during the past century.

The eventual decline and near extirpation of many of our larger mammals cannot be laid to any single cause. Insatiable greed and reckless slaughter by man with no thought to the future was surely one of the major causes of this decline. To be sure, the western plains could not support the livestock industry, the rolling miles of wheat, and the hordes of buffalo. These great hoofed creatures are now reduced to a few thousand semidomesticated animals herded on Federal and private reservations. A free herd in the Wood Buffalo National Park of Canada may be considered the only truly wild bison existing in North America.

Except for sporadic introductions, elk have disappeared from the East, and are now largely restricted to the mountain country of the West. By the turn of the century, beaver had all but disappeared from the eastern forests. Market hunting had been a notable instrument in the reduction of the deer. Settlement of the country encouraged large-scale agricultural operations, while the transcontinental railroad provided a ready means of getting wild meat to the eastern markets. The continuing demand for hides and pelts resulted in further inroads on our native mammals. Small wonder that state and Federal authorities and all interested in our natural resources were alarmed at the appalling destruction. Their concern is no less marked for species that today appear headed the way of the bison. Less than a half-century ago the great Merriam elk, unable to compete with cattle on the overgrazed range and susceptible to hunting pressure, disappeared forever. Is the end at hand for the little Key deer, *Odocoileus virginianus clavium*? Inhabiting an area only 17 miles long and 15 miles wide, this diminutive creature has the smallest range of any deer in the world. A full grown buck of this elfin race stands but 25 inches at the shoulder and weighs little more than 30 pounds. The entire population of the Florida Keys was estimated at 57 individuals in January, 1952.

The death knell has sounded for many North American mammals. The picture, however dark, is not quite one of such despair as many like to indicate. Much of the destruction of this natural heritage has been due to ignorance and thoughtlessness. It will be appropriate to consider some of our native mammals whose threatened extinction a few decades ago was of grave concern to the American public.

Few stories are more impressive in conservation history than that of our fur seals. The ravishment of the great herds had been carried on for nearly a century and a half when the Russian navigator, Gerassim Pribiloff, discovered, in 1786, the islands that bear his name. In that year, probably 4,000,000 seals occupied the rocky shores during the spring and summer months. Pelagic hunting by fishermen of Canada, the United States, and Japan had resulted in such reduction and waste that by 1910 not more than 130,000 animals remained of the former millions. In 1911, a treaty between Russia, Japan, Great Britain, and the United States put an end to pelagic sealing, and our country, owning the islands, assumed management of all sealing operations. A quarter-century later, the herds totaled 3,600,000 animals. Fish and Wildlife Service personnel cooperate with the Fouke Fur Company in handling the seal harvest. The animals are driven from their rocky hauling grounds to the flat tundra, where groups of immature males are cut out and the remainder allowed to return to the sea. The number annually killed is based on the size of the herd. The increasing returns from the sale of pelts (60,000 to 70,000 annually) and by-products has provided the government with a growing profit and at the same time assured a livelihood to the natives of these lonely shores.

The exploitation of the great whales followed a pattern of many another natural resource. In the early years of the past century, whaling was confined largely to coastal waters. Later the whalers ventured on all of the oceans of the world; the United States owes much to the intrepidity and fearlessness of the hardy whaling masters who first carried the American flag into new and little explored corners of the world. The decline in the number of whales has been evident for many years, but improved methods of hunting and handling the catch of whales and the utilization of by-products make whaling still profitable to those engaged in the industry. The fleet of vessels and floating refineries returning from the South Seas in 1930 brought the largest cargoes of sperm oil ever loaded. These whales were located and reported by wireless-equipped aircraft and killed by electric harpoons. It is fortunate that the leaders in the whaling trade are cooperating in an effort to obtain data on these cetaceans which will be helpful in evaluating the biological factors involved.

At the turn of the century, whalers began operating in the Antarctic Ocean, the last great unexploited area. In the early 'thirties the League of Nations called together a committee to consider international regulation of the whaling industry. Since this action, several international conventions have set forth regulations for whaling, the first in 1932 and another in 1937, upon which, with subsequent protocols and agreements, the present whaling regulations are chiefly based. These regulations prescribe seasons for whaling, establish the minimum legal size of each species, and prohibit the killing of females accompanied by calves, and of any whales of certain species. The regulations also require the fullest possible use of each whale taken. The participating nations, which include most of the important whaling countries, share responsibility for enforcement (Carson, 1948).

The history of the beaver in North America follows a pattern well known to conservationists. At one time it was widespread and abundant in the east but trapping pressure for the valued pelts brought it virtually to the brink of extermination. By 1900 New York and the New England states could boast of only a few dozen. Introductions of a few here and there resulted in an astonishing increase. In the early 'twenties, increasing complaints of damage indicated all too well the success of these introductions. The beaver is now actually a pest in many of the regions where it was a rarity a half-century ago. Through the flooding of valuable timberland this big rodent may actually prove a nuisance. The white-tailed deer is another striking example of a species that became so scarce in the early part of the present century that Easterners considered it no longer of significance as a game species. Introductions and closed seasons have now made this fine animal abundant in the East. Its unprecedented increase in recent years has been cause for much concern among agriculturists, for deer depredation in orchards and to crops is of no mean consequence.

Some Practical Considerations

With increasing human populations, it was apparent that the wildlife of North America would play an ever more important role. Environmental changes wrought by man resulted in far-reaching effects. Lumbering operations destroyed habitat for the moose and bear, while it created a more desirable habitat for the cottontail and fox. The resultant farmlands and second-growth timber provide a more suitable environment for many species that shun the solid stands of timber. Destruction of grasslands on the western prairies increased competition between rodents and livestock for the range. These changes have been reflected in many ways.

It is difficult, often impossible, to assess an animal in the economic ledger. The common field mouse plays a useful part in the economy of nature when it occupys waste lands. Here it provides food for a host of predators, transforming grass into fur coats. It may act as a buffer against predation on more desirable species. In the orchards and grain fields, its ravages are measurable; here it must be classed as a pest of the first order. We acknowledge the usefulness of the beaver in impounding waters and preventing rapid run-off. Its value in the past and present as a fur-bearer will not be denied. When the big rodent kills extensive tracts of valuable timber through flooding, or disrupts a water supply through interference with the normal water level, then we must take steps to control the animal. The cottontail rabbit is hailed as our primary game animal in the eastern states, yet its depredations in the orchard or garden are often severe. It must now be apparent that a decision regarding the economic value of a species is difficult, indeed, often impossible, in the light of our present knowledge. Judgment of any species must take into consideration many factors, two of the most important being time and place.

We may consider several categories, when attempting a critical judgment of the economic worth of a species.

The esthetic value of many mammals cannot be denied. Many thousands of tourists visit our National Parks annually. Wild animals, be they elk, bear, wild sheep, or the teeming populations of smaller species, share with the geysers, waterfalls, and great forests the interest of the people. Summer visitors to our eastern parks delight in the sight of a beaver dam, and drive many miles in the hope of catching a glimpse of a doe with her fawns on some wilderness meadow. Residents of Vilas County, Wisconsin, realizing the recreational value of wildlife to the tourist, posted thousands of acres against hunting. These people realized that deer were a greater asset to them alive and brought a larger reward through summer trade than nonresident hunters could possibly do. In 1946, over 21,000,000 people visited the 160 acres of the National Park system. They came to see our native mammals as well as the other natural wonders.

Perhaps more tangible values are to be found in the hunting and trapping of game and fur-bearing species. An increasing number of hunters take to the fields each year. It is fortunate for them that many game species have shown a like increase in numbers.

The exploitation of our fur resources is woven inextricably with the settlement of the great Mississippi Basin and the West. We have seen that the resultant changes in environment have been responsible for the decline of many species, while others have increased wherever man has partly cleared the forests and farmed the land. Some species are adaptable and can thrive in arable lands, whereas others depend upon wilderness areas. Trapping is big business and provides a partial livelihood to many thousands of Americans. In the early 'forties, trapper income was estimated at no less than $100,000,000 annually. While this may appear to be a relatively small figure in so far as products of the land are concerned, the return is very substantial. The money is distributed among the low income group and at a season when a cash crop is most needed. The fur industry is a huge one, employing many people who are directly dependent on this great resource.

Except for the muskrat and the beaver, we know less about the habits and needs of our fur animals, than we do of the game species. This lack of knowledge may be attributed to several factors. Most important, perhaps, has been the almost universal belief that fur-bearers and vermin are synonymous. This has been particularly true of the weasel, mink, skunk, fox, and other carnivores. The apathy of state game officials has been marked. Fur animals have brought little or no revenue to the state treasuries, hence research on, and legislation for, this valuable resource has not until recently received the attention it merits.

The annual loss to crops, forage, and forests occasioned by our native mammals is a very real one. Bell (1921) has placed this monetary loss at $300,000,000. By far the larger share of this loss may be levied against pocket gophers, ground squirrels, field mice, cottontails and jackrabbits, with cotton rats, porcupines, woodchucks, moles, and other species adding to this destruction. It is a well known fact that wild mammals may transmit virulent diseases to man and his livestock. The study of the diseases of wild mammals is still in its infancy; man and his domestic animals frequently contract these diseases. When outbreaks of rabies, tick fever, or endemic typhus break out among feral species, it has been found necessary, often at considerable expense, to conduct extensive campaigns against these animals. Such wholesale slaughter is regrettable but inevitable when considerable monetary loss or a threatened human pandemic appears imminent. When the 1924 outbreak of hoof-and-mouth disease occurred in California, more than 22,000 deer were poisoned on the Stanislaus National Forest of California. The disease was checked, and the deer soon regained their former abundance.

Mammalian Research

It was inevitable that research studies should emphasize the species which are of economic significance. Following the early trend of systematic mammalogy, when species were described, their distribution plotted, and their practical significance determined, emphasis was directed toward the acquisition of detailed knowledge concerning individual species. With the essential features of the distribution of most of our commoner species mapped, the main categories in the life histories have been catalogued, if only in a brief, superficial manner. To be sure, this advance in our knowledge of the rich North American mammalian fauna has not kept pace with the more numerous bird species, but the reason is quite apparent.

In the early years of field investigation, emphasis was placed on regional lists, annotated with brief accounts of the habits of the included species. These reports followed the pattern of some of the early North American Fauna series. In these

Figure 2. By their numbers alone, the teeming hordes of ground squirrels in western North America provide an unparalleled opportunity for research. Behavior, activity and population studies, to cite a few, are indicated by the abundance of these little mammals. The golden-mantled ground squirrel, *Citellus lateralis*, was photographed in Estes Park, Colorado, on July 1, 1941.

reports, emphasis was placed on the distribution of species, but much new material on habits was included. The detailed studies currently being conducted on the larger mammals are noteworthy. Federal and state funds have been made available for these researches. In 1949, thirty-four states were engaged in deer research alone. While duplication of effort is inevitable in such widespread investigations, the end results may well justify these many studies.

Many notable contributions have been made on the life history of a single species, but in the present brief summary, mention can be made of only a few. Paul Errington's muskrat studies are of major import. His principal objective has been to fathom the rules of order governing the distribution and maintenance of populations in different types of habitat. The studies of Lee R. Dice, of the University of Michigan, and his students, notably W. Frank Blair, on speciation in *Peromyscus* indicate the value of long-time research on a single genus. The laboratory studies of Dice support the keen taxonomic judgment of the late Wilfred Osgood, whose revision of the genus is an unparalleled systematic study.

The present trend is not so much an effort to catalogue the details of a particular species, but rather to attempt interpretations in the light of relationships. We must now inquire into the "why" rather than solely occupying ourselves with observed facts. A classic account of field observation has been the documentation of the behavior of the red deer (Darling, 1937). This report should be studied by all naturalists. The publication of Charles Elton's *Animal Ecology* in 1927 lent great impetus to the study of population dynamics. Presently a score of American investigators are following his leadership in this important field. The development of banding or marking animals so that they might be recognized when recaptured has been of inestimable value in determining many biological features. This subject, together with territorialism, was first studied among the birds by H. E. Howard. The initial studies on mammals in this field were made by W. H. Burt, of the University of Michigan.

Systematic mammalogy has undergone a marked change in the century under review. Earlier taxonomists were content to describe a new species in a few hundred words, expressing little concern for the relationships that existed between the new form and its close relatives. The concept of modern taxonomy rests in an expression of relationship, based on the study of large series and firsthand knowledge of the habitat in which the species lives. An excellent example is the recent study of the harvest mice by Hooper (1952).

The American Society of Mammalogists

The early interest in ornithology and entomology may, in a measure, be attributed to several factors. Their subjects attract the eye, they are everywhere to be seen, and their great variety and the relative ease of collecting them attracts the young naturalist. The making of collections and the exchange of specimens has had a stimulating effect on the development of natural history in North America. We have seen how the development of the snap-back trap had a salutary effect on the growth of mammalogy. The time was ripe for the organization of a society, the function of which would be to encourage interest in mammals and provide a means for the publication of original research. Botanical, entomological, and ornithological societies were flourishing in the early years of the present century, but there was yet no organization devoted solely to the study of mammals.

The American Society of Mammalogists was founded at Washington, D. C., on April 3, 1919. When a call was issued for a meeting at the U. S. National Museum on that date, sixty persons from many parts of the United States and Canada were present for the initial session. Plans for the society were perfected, officers elected, committees formed, and by-laws and rules were adopted. The objects of the infant society were declared to be "the promotion of the interests of mammalogy by holding meetings, issuing a serial or other publications, aiding research, and engaging in such other activities as may be deemed expedient." Systematic work, life history and habits of mammals, evolution, paleontology, anatomy, and every phase of popular and technical mammalogy were to be within the scope of the society and its publication. One of the declared objects of the society was to be the publication of the *Journal of Mammalogy*. This publication was planned to be indispensable to all workers in every branch of mammalogy and of value to every person interested in mammals, be he systematist, paleontologist, anatomist, museum or zoological garden man, sportsman, big game hunter, or just plain naturalist.

How well the aim has been fulfilled is attested by the breadth and wide scope of articles that have appeared in the thirty-three volumes of this quarterly. The first officers and directors are a virtual roster of the great names in American mammalogy thirty years ago. Merriam was honored with the presidency, a fitting tribute to his lifetime contributions in the field. E. W. Nelson and Wilfred H. Osgood were vice-presidents, Hartley H. T. Jackson the corresponding secretary, Walter P. Taylor, treasurer, and Ned Hollister the editor. Members of the council (now known as directors) included Glover M. Allen, Rudolph M. Anderson, Joseph Grinnell, Marcus W. Lyon, Jr., W. D. Matthew, John C. Merriam, T. S. Palmer, Edward A. Preble, and Witmer Stone. Of this group, Nelson, Osgood, Matthew, Allen, Stone, Lyon, Grinnell, Jackson, and Taylor all were elected to the presidency of the society in recognition of their contributions to mammalogy. The society has published several monographs, including the *Anatomy of the Wood Rat* by A. B. Howell, *The Beaver: Its Work and Ways* by E. R. Warren, and *Animal Life of the Carlsbad Caverns* by Vernon Bailey.

The Society has a current membership of more than 1,350 individuals.

The Pacific Northwest Bird and Mammal Society was founded January 7, 1920. One of the objects of the society was to promote interest in the scientific study of birds and mammals within the region mentioned. The *Murrelet,* official publication of the society, is published triannually. Except the American Society of Mammalogists, this is the only organization in the United States which expressly designates the professional field of mammalogy as one of its primary aims.

In Germany, the Deutschen Gelleschaft für Saugetierkunde, organized in 1926, publishes the *Zeitschrift für Saugetierkunde.* The French journal *Mammalia* has gone through sixteen volumes. In content, these two important journals follow the leadership of the *Journal of Mammalogy.*

We would be remiss, indeed, if no mention were made of the many other societies that have not only professed an interest in mammals, but, by militant effort, have helped further interest in our native species. The National Audubon Society, aware of the plight of many of our rarer mammals, has been increasingly concerned with conservation problems. Among Federal agencies, the Soil Conservation Service, the Bureau of Animal Industry, the Bureau of Entomology and Plant Quarantine, the National Park Service, and the Forest Service all are interested in the several biological fields which include consideration of mammal life. In close cooperation with the Fish and Wildlife Service, they are directly responsible for research that often includes the study of mammals.

Present Needs

Surely it is evident that many pressing problems of utmost economic significance and academic interest have yet to be solved. Research on our native mammals, except within recent years, has not been extensive. It is lamentably true that problems dealing with mammals currently arise, some of great importance, that cannot be answered with authority. Training in mammalogy is as necessary to those who would consider it a profession as it is in other allied fields. A knowledge of botany, entomology, geology, mathematics, and kindred subjects must be considered a part of the training of the professional investigator.

In earlier years, a few recognized masters guided the destiny of many an untrained youth into the field in which he later excelled. The professional mammalogists of the past century were primarily trained in medicine, as were Merriam, Mearns, and Coues. Others had no formal training in the sciences. Vernon Bailey is an illustrious example of a self-taught naturalist who gave inspiration to the generation that followed.

In the early part of the present century, few educational institutions were concerned with specialized courses in natural history. The classic instruction included anatomy, physiology, and embryology, for the prescribed curriculum was designed for premedical training. The influence of Agassiz, Jordan, and their disciples was destined to foster the study of living animals. In the training of a naturalist, be he interested in systematics, morphology or life histories, a sound biological basis is the best preparation. Few will deny this assumption.

University courses in the natutral history of vertebrates, in which the study of mammals was included, were given a half-century ago. Notable among the institutions that gave special instruction in mammalogy in the early years of the present century should be mentioned the University of California, Cornell University, and the University of Michigan. Presently thirty or more colleges give courses that deal with mammals, while many others offer instruction in vertebrate natural history. Mammal studies are emphasized in many schools that include wildlife courses in their curriculum. These, of necessity, differ widely in the various institutions where such instruction is offered.

Ever since the first World War, when attention was focused on the alarming state of our natural resources, including wildlife, the growth of both Federal and state agencies concerned with the management and conservation of these resources has been marked. Instruction in the universities has kept apace with the increased demand for trained personnel to fill the positions in this expanding field. While mammalogy is only a small part of the wildlife field, there is a constant demand for individuals with specialized training in this subject. In government, state, and educational institutions, the training requirements are rigorous and selective. Only the ablest candidates are assured of a position.

Since these are career positions, promotions are usually slow, and salaries are not comparable to those of the other professions.

Positions in the field of mammalogy are not numerous, and the prospective student planning a career in this branch of zoology should examine carefully the opportunities before embarking on a specialized course. Basic training in the natural sciences, including mathematics, geology, chemistry, physics, and the usual undergraduate courses in biology, are a primary requisite to advanced study. Graduate study is desirable, but not of paramount importance if the individual has a broad concept of the field. This is usually acquired during the early years and follows the usual pattern of collecting and an interest in a particular group, be it plant or animal.

In an interesting report on this subject Miller (1928) stated:

> As now used, the term mammalogy applies primarily to what is known as the systematic study of mammals, the main object of which is to find out exactly how many kinds of mammals there are in the world, exactly where each kind lives, and exactly what are the relationships of these creatures to each other and to their predecessors now gone from the ranks of living things.

Included are systematics, distribution, and paleontology. Miller's definition of the science of mammalogy does not consider the economics, ecology, and life history of the mammals. The present trend in research is partially evident in a review of the past eleven issues of the *Journal of Mammalogy*. Of 118 major articles, more than half deal with the life history or habits of mammals, morphology accounts for 10 per cent, and systematics and distribution 8.5 per cent respectively. Since there appear to be somewhat fewer publication sources for the accounts of habits than for those on systematics, this evaluation does not give an accurate trend in mammal studies currently in progress. It does, however, suggest the broad interests of the investigators presently engaged in mammal research.

The advance in our knowledge of systematics and distribution has been particularly gratifying. Nevertheless, a promising field of investigation awaits those who are willing to spend long hours afield, collecting and observing in their natural haunts almost any species of North American mammal. The increasing number of young men and women that are being attracted to the study of mammals will surely have a salutary effect on the progress of mammalogy in North America.

LITERATURE CITED

Allen, Glover M.

1942. Extinct and Vanishing Mammals of the Western Hemisphere with the Marine Species of all the Oceans. Spec. Publ. No. 11. vii–xv + 620 pp.; illus. New York: American Comm. for International Wildlife Protection.

Anderson, Rudolph Martin

1946. Catalogue of Canadian recent mammals. Nat. Mus. Canada. Bull. 102, pp. 1–238.

Anthony, Harold E.

1928. Field Book of North American Mammals. iii–xxvi + 674 pp. 150 figs. 48 pls. New York: G. P. Putnams Sons.

Asdell, S. A.

1946. Patterns of Mammalian Reproduction. v–x + 437 pp. illus. Ithaca: Comstock Publ. Co.

Audubon, John James and John Bachman

1845–1854. The Viviparous Quadrupeds of North America. Vol. 1: vii–xiv, 1–389; Vol. 2, 1–334; Vol. 3, i–iii, 1–348. New York: V. G. Audubon.

Bailey, Vernon

1907. Wolves in Relation to Stock, Game and the National Forest Preserves. Forest Service Bull. No. 72.

1931. Mammals of New Mexico. 412 pp. illus. North American Fauna 53. Bur. Biol. Surv., U. S. Dept. Agric. Washington, D. C.

1936. The Mammals and Life Zones of Oregon. 416 pp., illus. North American Fauna 55. Bur. Biol. Surv., U. S. Dept. Agric. Washington, D. C.

Baird, Spencer Fullerton

1857. Mammals: General Report upon the Zoology of the Several Pacific Railroad Routes. Repts., Explorations and Surveys for Railroad Route from Mississippi River to Pacific Ocean. 8 (pt. 1): xix–xlvii, 1–757, pls. 17–60. Washington, D. C.

Beddard, Frank Evers

1902. Mammalia. v–xii + 605 pp., 285 figs. London: Macmillan Co.

Bell, W. B.

1921. Death to rodents. Yearbook U. S. Dept. Agr. (1920), pp. 421–438, illus.

Bourlière, F.

1951. Vie et Moeurs des Mammiferes. 249 pp. illus. Paris: Payot.

Burt, William Henry

1946. The Mammals of Michigan. vi–xv + 288 pp. illus. Ann Arbor: Univ. Michigan Press.

Burt, William Henry and Richard P. Grossenheider

1952. A Field Guide to the Mammals. v–xxi + 200 pp. illus. Boston: Houghton Mifflin Co.

Cabrera, Ángel

1922. Manual de Mastozoología. vii–xi + 440 pp. illus. Madrid and Barcelona: Compania Anonima de Libreria.

Cahalane, Victor H.

1947. Mammals of North America. vii–x + 682 pp. illus. New York: Macmillan Co.

Carson, Rachel L.

1948. Guarding Our Wildlife Resources. Conservation in Action, No. 5, Fish and Wildlife Service. Washington, D. C.

Cope, Edward Drinker

1884. The Vertebrata of the Tertiary Formations of the West. Book 1. Report of the U. S. Geological Survey of the Territories. (F. V. Hayden.) Vol. 3. xxxv + 1009 pp., 75 pls.

Dalquest, Walter W.

1948. Mammals of Washington. Vol. 2:1–444, 140 figs. Univ. Kansas Publ. Mus. Nat. Hist.

Darling, F. F.

1937. A Herd of Red Deer. 240 pp. Cambridge: Oxford University Press.

Davis, William B.

1939. The Recent Mammals of Idaho. 400 pp. illus. Caldwell, Idaho: Caxton Printers.

Dekay, James E.

1842. Zoology of New York. Pt. 1. Mammalia. vi–xii + 146 pp., 36 pls.

Desmarest, A. G.

1820. Mammalogie ou description des especes. Paris.

Doutt, J. Kenneth, A. Brazier Howell, and William B. Davis

1945. The Mammal Collections of North America. Journ. Mammal. 26:231–272.

Flower, William Henry, and Richard Lydekker

1891. An Introduction to the Study of Mammals Living and Extinct. v–xvi + 763 pp., 375 figs. London: Adam and Charles Black.

Godman, John D.

1826. American Natural History, or Mastology. 3 vols. Philadelphia: H. C. Carey and I. Lee.

Gregory, William K.

1910. The Orders of Mammals. Bull. Amer. Mus. Nat. Hist. Vol. 85, 350 pp.

Grinnell, Hilda W.

1943. Bibliography of Clinton Hart Merriam. Journ. Mammal., 24:436–457.

Grinnell, Joseph, Joseph S. Dixon, and Jean M. Linsdale

1937. Fur Bearing Mammals of California. Vol. 1, vii–xii + 375 pp. Vol. 2, vii–xiv + 400 pp. illus. Berkeley: University of California Press.

Hall, E. Raymond

1946. Mammals of Nevada. v–xi + 710 pp. illus. Berkeley: Univ. Calif. Press.

Harlan, Richard

1825. Fauna Americana. x, 11–318. Philadelphia: A. Finley.

Harper, Francis

1927. Mammals of the Okefenokee Swamp region of Georgia. Proc. Boston Soc. Nat. Hist. Vol. 38, no. 7, pp. 191–396. Boston.

1945. Extinct and Vanishing Mammals of the Old World. Spec. Publ. No. 12. x–xv + 850 pp., 67 figs. New York: American Comm. for International Wildlife Protection.

Henderson, Junius, and Elberta L. Craig

1932. Economic Mammalogy. v–x + 397 pp. Baltimore: Chas. C. Thomas.

Hooper, Emmet T.

1952. A systematic review of the harvest mice (genus *Reithrodontomys*) of Latin America. Misc. Publ. Mus. Zool. Univ. Mich. No. 77, pp. 1–225, illus.

Jordan, David Starr

1929. Manual of the Vertebrates of the Eastern United States. Thirteenth Edit., vii–xxxi, 446 pp. illus. New York: World Book Co.

Kellogg, Remington

1946. A century of progress in Smithsonian biology. Science, 104(no. 2693):132–141.

Kennicott, Robert

1858. The quadrupeds of Illinois injurious and beneficial to the farmer. Rept. Commiss. Patents (1857), pp. 72–107.

LEIDY, JOSEPH

1869. The Extinct Mammalian Fauna of Dakota and Nebraska including an Account of Some Allied Forms from Other Localities, together with a Synopsis of the Mammalian Remains of North America. Journal of the Academy of Natural Sciences Philadelphia, ser. 2, Vol. 7, 472 pp., 30 pls. Philadelphia.

LYON, MARCUS WARD, JR.

1936. Mammals of Indiana. Amer. Midl. Nat. 17:1–384.

MERRIAM, CLINTON HART

1884. The Mammals of the Adirondack Region. 316 pp. New York: Privately published.

MERRIAM, C. HART, and LEONHARD STEJNEGER

1890. Results of a Biological Survey of the San Francisco Mountain Region and the Desert of the Little Colorado, Arizona. North American Fauna. No. 3. Bur. Biol. Surv., U. S. Dept. Agr. 136 pp., 14 pls., 5 (col.) maps.

MILLER, GERRIT S. JR.

1924. List of North American Recent Mammals, 1923. U. S. Nat. Mus. Bull. 128. xvi + 673 pp. Washington, D. C.

1928. Mammalogy and the Smithsonian Institution. Ann. Rept. Smithson. Inst. Publ. 2981, pp. 391–411.

NELSON, E. W.

1916. The Larger North American Mammals. Nat. Geog. Mag. vol. 30:385–472.

1918. Smaller Mammals of North America. Nat. Geog. Mag., vol. 33:371–493.

OSBORN, HENRY FAIRFIELD

1910. The Age of Mammals in Europe, Asia and North America. xx + 635 pp. New York: Macmillan Co.

1916. Men of the Old Stone Age, Their Environment, Life and Art. xxvi + 545 pp. New York: C. Scribner & Sons.

1929. The Titanotheres of Ancient Wyoming, Dakota and Nebrasks. Monogr. U. S. Geol. Surv., No. 55, Vol. 1, pp. i–xxiv, 1–701, 42 pls. Vol. 2, pp. i–xi, 702–953, 193 pls.

OSGOOD, WILFRED H.

1943. Clinton Hart Merriam—1855–1942. Journ. Mammal., 24:421–436, 1 pl.

SCOTT, WILLIAM B.

1913. A History of Land Mammals in the Western Hemisphere. ix–xiv, 693 pp., 304 figs. New York: Macmillan Co.

SIMPSON, GEORGE GAYLORD

1945. The Principles of Classification and a Classification of Mammals. Bull. Amer. Mus. Nat. Hist. Vol. 85. xvi + 350 pp.

TROUESSART, EDOUARD LOUIS

1897–1905. Catalogue mammalium tam viventum guam fossilium. Six parts, 1469 pp. Berlin: R. Friedlander und Sohn.

WEBER, MAX

1904. Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. xii + 866 pp., illus. Jena: Gustav Fischer.

INVERTEBRATE PALEONTOLOGY AND HISTORICAL GEOLOGY FROM 1850 TO 1950

By CHARLES E. WEAVER

For a proper understanding of the development of invertebrate paleontology and historical geology from 1850 to 1950 a review of the important trends in research during the first half of the nineteenth century is essential. The early contributions which laid the foundations of these sciences originated for the most part in Europe, although there was marked advance in North America between 1830 and 1850.

Invertebrate Paleontology Prior to 1850

The publication of the tenth edition of *Systema Naturae* by Linnaeus in 1758 laid the foundation of modern systematic zoology and invertebrate paleontology. Over 4,200 different kinds of animal life were listed, briefly described, and classified according to a binomial system in which each form was given a generic and specific name. Linnaeus considered a species as composed of individuals descended from ancestors with common morphological characters and held that each separate species possessed certain immutable characters which remained constant and were not subject to modification. Interbreeding was possible only among individuals of the same species. This concept of a species strongly influenced contemporary students of organic life during the later years of the eighteenth century and the earlier decades of the nineteenth.

Among the more important contributors to the development of paleontological science following Linnaeus was Georges Cuvier of France. Although his investigations were largely confined to fossil vertebrates, the principles developed were applicable to the invertebrates also. His earlier work involved a study of the anatomy of fossil bones of elephants from the Paris Basin and emphasis was placed on the differences in the skeletons of living forms in the collections of the Paris museums. He called attention to the evolution of these organisms. The first quarter of the nineteenth century was devoted to a comparative study of the osteology of the fossil remains of amphibians, reptiles, and mammals from the Tertiary deposits of Europe and a comparison of these bones with those of living representatives. The results of these important studies appeared in a four-volume work first published in Paris in 1811–1812. The significance of this contribution was the establishment of the law of correlation of parts. According to this law all the different components of the skeleton of an organism are morphologically related and a modification of one part would present corresponding differences in the other correlated parts. Many new genera and species from the Upper Eocene of the Paris Basin were described. The importance of this new procedure in the investigation of fossil remains is evident in the character of published work throughout Europe during the second quarter of the nineteenth century.

Cuvier emphasized the occurrence of the more primitive forms of animal life in the older geological formations and pointed out that extinct genera lived at an earlier time than those of the Recent. However, he did not believe that the living organisms had originated through the anatomical modifications of the older forms. He considered that during the past history of the earth there had been many sudden and violent disturbances of the crust which had resulted in the submergence of vast areas of land and the reappearance from beneath the ocean's surface of vast islands and continental masses. Destruction of the faunas and floras accompanied these catastrophic movements. Following each catastrophe a new and more advanced biologic fauna came into existence, the last of these appearing about six thousand years ago. Translations of Cuvier's work into several languages accentuated discussion of the problem. The Cuvierian concept of immutability of species was opposed by several European naturalists who held that new species might arise by the gradual modification of pre-existing species as the result of changing environments. This became known as the theory of mutability in contrast to that of immutability as advocated by Cuvier.

Among the earliest strong supporters of the concept of mutability of species was Lamarck, who developed the idea that the morphological characters of a species might be subject to modification from generation to generation when subjected to environmental stimuli and that such acquired characters could be inherited. He recognized the morphological differences of extinct species from a succession of epochs and compared them with species now living in nearby areas and thus pointed out the possibility of the correlation of formations by the use of fossils. His investigations were largely concerned with marine invertebrate fossils from the Tertiary deposits of the Paris Basin, which were described (Lamarck, 1815–1822) in his important monograph on *Natural History of Invertebrate Animals.* This contribution, devoted largely to fossil mollusks, played an important part in the foundation of scientific conchology. Although the Lamarckian concepts were accepted by an increasing number of European investigators yet the Cuvierian ideas were strongly entrenched in scientific thinking even beyond the middle of the nineteenth century and to a considerable extent influenced the writings of d'Orbigny.

Many significant contributions were made to the growing science of paleontology during the early half of the nineteenth century. These consisted largely of descriptions of fossil species and monographs of faunas from different formations of Europe and North America, together with catalogues containing named species. Among the important contributors were James Sowerby and his son, James de Carle Sowerby, E. F. Schlotheim, H. G. Bronn, G. A. Goldfuss, A. d'Orbigny in Europe, and T. A. Conrad in North America.

The mollusks of Great Britain were described and illustrated in a six-volume work by the Sowerbys published from 1812 to 1846. This work was of great value for further investigations in conchology and for a comparison of the Tertiary faunas of Great Britain with those of France and other parts of Europe. Contemporaneously in Germany Ernst von Schlotheim in 1820 published his work *Die Petrefactenkunde,* in which many invertebrate fossils were figured and described according to the binomial nomenclature. This work was important for those who were later concerned with problems of taxonomy. The rapid appearance of published descriptions and illustrations of fossils were followed in 1834–1838 by a summary of the known information concerning paleontology and stratigraphy in H. G. Bronn's *Lethaea Geognostica* and his *Index Palaeontologicus* in 1848–1849. These works were of fundamental importance to many of the investigations carried on during the middle of the nineteenth century. The *Petrefacta Germaniae* of Goldfuss and Munster carries descriptions and illustrations of fossil echinoids, mollusks, corals, and sponges collected largely in Germany. The publication of d'Orbigny's *Paléontologie française* began in 1840 and continued till 1855. It was his intention to include a description with illustrations of all the fossils found in France but it was confined largely to Jurassic and Cretaceous echinoids, brachiopods, gastropods, and cephalopods.

In North America James Hall had published several monographs on the Paleozoic fossils of New York State but most of his contributions appeared during the second half of the century. Intensive investigation of Tertiary mollusks was initiated by T. A. Conrad in 1832–1833 in his work on the fossil shells of the North American Tertiary. The first Tertiary fossil collections made on the Pacific Coast were submitted to him for identification and age determination and initiated a series of investigations which have been in progress for over one hundred years. It is of interest to note that Conrad followed the Cuvierian concept of species and believed that the fauna of each period of geologic time suffered annihilation as the result of climatic and other environmental changes, new faunas being developed in the following period.

By the middle of the nineteenth century the Cuverian concept that the faunas of each geologic period had no species in common with those which preceded and followed it was gradually abandoned as information became available that transitional genera and species partially filled the gaps and that the time span for each showed great variations. Although d'Orbigny, Agassiz, and others still supported in varying degrees the views of Cuvier, the evidence presented by Bronn that the faunas of each period resulted from the modification of species of the preceding period, together with the uniformitarian ideas advocated by Lyell concerning earth history, laid the groundwork for the gradual acceptance of Darwin's theory of evolution. The prevailing concepts of the more purely biological aspects of paleontology in 1850 were developed largely from the contributions of the above-mentioned investigators and thus were laid the foundations for a rapidly expanding science of paleontology.

Historical Geology Before 1850

The prevailing ideas concerning stratigraphy at the opening of the nineteenth century largely resulted from the influence of the earlier teaching of A. G. Werner in Germany. Contemporary publications were largely of a descriptive nature, with emphasis on places of occurrence, thickness of layers, and mineralogical composition of the rock. The importance of the use of fossils in determining the age of the strata had not been considered. The science of stratigraphy was established in England early in the nineteenth century as the result of detailed field studies by William Smith. Without formal training

Smith devoted many years to the tracing of surface outcrops of different layers of slightly tilted strata across a part of England and collected and kept separate the fossils from each stratum. He recognized that each stratigraphic unit was characterized by a set of genera and species and that these faunas differed one from the other in the succession of beds from the base to top. He found that a single stratum when followed for long distances along the surface contained the same assemblage of species and that any particular isolated layer of rock could be identified by the fossils within it as belonging to a certain bed within a succession of strata. The trends of each stratigraphic member were drawn in color on maps with sections showing the sequence of layers as they passed beneath the surface. These maps, published with an explanatory text (W. Smith, 1815), constitute the first large areal geologic map. It served as the foundation of a new epoch for the presentation of the results of field work and stratigraphic research to the scientific public, and opened a wealth of accurate information to the geologists of the Continent who were concerned with unraveling the geologic history of Mesozoic rocks.

Conybeare and Phillips (1822), following the principles set forth by Smith, published the results of their investigations in England and Wales and classified strata ranging in age from middle Paleozoic to Recent. The terms Eocene, Miocene, and Pliocene later introduced by Charles Lyell were not employed but rocks corresponding to these ages were recognized and referred to according to their mineral composition. The Cretaceous was divided into upper and lower units and the Jurassic into the Oolitic system and the Lias, the former being subdivided into upper, middle, and lower Oolite. The New Red Sandstone beneath the Oolitic was placed in the lower Mesozoic and above a fourfold division of the Carboniferous, the upper part of which was considered as equivalent to the Zechstein of Germany. The Old Red Sandstone was included within the Carboniferous until later assigned to the Devonian by Sedgwick and Murchison. The lower Mesozoic in Germany was studied in detail by various workers and divided into three members with the Bunter sandstone at the base, the Muschelkalk limestone in the middle, and the Keuper at the top; in 1834 the name Triassic was applied to the group by Alberti. The absence of the marine middle member in Great Britain was early recognized by British geologists.

In England, below the Old Red Standstone and above the granites and crystalline schists are a series of slates, limestones, and indurated sandstones which have suffered intense deformation. These rocks were studied by Sedgwick and Murchison and ultimately classified as the Cambrian and Silurian systems. The scarcity of fossils and the complexity of the stratigraphy rendered it impossible at first to establish the boundary between the two systems, with Murchison and Sedgwick becoming bitter enemies over the Cambrian. Murchison later (1839) included the entire assemblage of strata in the Upper and Lower Silurian and considered Sedgwick's Cambrian as a part of the Lower Silurian. Ultimately, however, Sedgwick's Cambrian was shown to be distinct from the Silurian. In 1879 the Lower Silurian rocks were studied by Lapworth and placed in a new system which he named the Ordovician. Meanwhile the Continental geologists examined the middle Paleozoic rocks in Germany, Belgium, Austria, and Scandinavia and attempted to make correlations with the succession of strata established in Great Britain by Sedgwick and Murchison. Among the more important of these investigations were those of C. F. Roemer (1844) on the faunas and stratigraphy of the Silurian and Devonian rocks of the Rhineland.

The classification of the less deformed upper Paleozoic rocks in Great Britain into Old Red Sandstone, Carboniferous Limestone, Millstone, Grit, and Shales, and Coal Measures earlier in the century had been established by Conybeare and Phillips and named the Carboniferous system. The geographical extension of these limestones into Belgium afforded an opportunity for an intensive study of the faunas by de Koninck in 1844. The occurrence of similar limestones in the eastern Alps was noted by von Buch in 1824. The uppermost Paleozoic rocks in Germany were termed the Zechstein and consist of a succession of shales, sandstones, and conglomerates which pass upwards into limestone, dolomite, and marl. These rocks which underlie the Triassic were investigated early in the nineteenth century and the Zechstein group was considered as equivalent in age to the Magnesian Limestone of England. The rocks of late Paleozoic age in the Ural Mountains of Russia had been studied by several geologists and the resulting published maps drew attention to this area as worthy of special investigation. Accordingly, Murchison, who already had examined many areas in the Alps and other parts of Europe, was requested by the Russian government to make a geological study of the Province of Perm. He was accompanied by the French geologist, de Verneuil, and the Russian Count, von Keyserling. The results of this investigation were published in 1845 in their monograph, *The Geology of Russia in Europe and the Ural Mountains.* The rocks which overlie the coal-bearing beds were called the Permian system.

The marked variations in the lithologic character of the faunal facies of the Cretaceous rocks in different parts of Europe in contrast to the greater uniformity prevailing among the Jurassic resulted in the development of several distinct forms of classification and nomenclature. Numerous important contributions were published before the middle of the nineteenth century and the succession of formations in each country was fairly well established. By 1850 the broad outlines of the stratigraphical and faunal classification of the Cretaceous deposits were somewhat similar to those in use at the present time and served as a foundation for more detailed research in other parts of the world from 1850 to 1950.

In England the sedimentary rocks lying between the basal Tertiary and Upper Jurassic were classified by William Smith in downward sequence as the White Chalk, Gray Chalk, Greensand, and Micaceous Clay. Certain dark clays occurring locally beneath the Greensand were called the Blue Clay but were later designated the Gault. Later investigations by Fitton in eastern Sussex showed that a portion of the lower Greensand passed from a marine to fluviatile facies. This was termed the Wealden formation. These deposits contain a rich flora and the remains of fossil reptiles. The name Speeton clay was given to beds in Yorkshire equivalent to the lower Greensand. The Upper Cretaceous or White Chalk was recognized as extending eastward into Belgium, France, Denmark, North Germany, and Poland.

The Cretaceous stratigraphic and faunal units of Great Britain are widely represented in France but the complete sequence of beds is not everywhere present. There is a prevailing similarity of the upper White Chalk and marls but the middle and lower members often present marked differences in lithology. Early in the nineteenth century Lower Cretaceous shales, limestones, and marls had been recognized as resting on uppermost Jurassic deposits in the Jura Alps of eastern France and in 1835 these rocks and their fauna were described and designated as Neocomian. The Cretaceous rocks and faunas in particular areas of France were studied by Leymerie, d'Archiac, and others and compared and correlated with the divisions established in England, Germany, and Switzerland.

During the first half of the nineteenth century, the Cretaceous deposits of Germany were studied by F. A. Roemer and Hans Geinitz. The former in 1841 published his great work on the Cretaceous of North Germany, with a description of the faunas and a classification of the rocks. At approximately the same time Geinitz described the Cretaceous faunas and rocks of Saxony and Bohemia. By the middle of the century the first volumes of d'Orbigny's *Paléontologie française* had appeared. In this work the French Cretaceous was divided into seven stages designated as Neocomian, Urgonien, Aptien, Albien, Gault, Cenomanien, Upper Greensand, Turonien, and Senonien. Additional investigations by Geinitz and Beyrich extended the German classification to the Cretaceous deposits farther east in Hungary and north into the Baltic region.

The results of early investigations of the richly fossiliferous Tertiary deposits of the Paris Basin led to a preliminary classification of the strata and a knowledge of the stratigraphic relationships of the invertebrate faunas occurring in the beds which later were to be designated as Eocene and Oligocene. An important contribution by Cuvier and Brongniart was published in 1808 and reprinted in 1811, in which the faunas were listed and the rocks described. Accompanying preliminary geologic maps and stratigraphic sections revealed the relatively simple structural features of the strata and some information concerning changing lithologic facies. The recognition of lower beds of plastic clay, followed by sandstones and limestones forming a group characterized by great numbers of *Nummulites,* led to the introduction of the term Nummulitic Series for strata which later were to be classified as Eocene. Above was a second group, which in upward succession consisted of gypsum, fresh water marls, and clays, passing upward into marine limestones and sandstones alternating with fluviatile and lacustrine beds. From such evidence Cuvier and Brongniart concluded that at the close of the Cretaceous, the area of the Paris Basin was only slightly above sea level and that it possessed an irregular surface formed by erosion of the Upper Chalk and that it was traversed by several streams. A local, differential, slight downwarping of the surface at the close of the Cretaceous permitted marine waters to transgress slowly into the river valleys and ultimately over the intervening land areas, thus permitting the deposition of fluviatile and lagunal deposits and the plastic clay. Intermittent advances and retreats of the sea were regarded as being responsible for the alternations of continental and marine beds and variations in sedimentary facies.

The Tertiary of the Belgian Basin was laid down in the northeast extension of the Paris Basin. One of the most important studies on these deposits was by A. Dumont (1849) in which the entire Belgian Tertiary succession was classified stratigraphically upward as the Heersien, Landenien, Yprésien, Panisélien, Bruxellien, Laekien, Tongrien, Rupelien, Bolderien, Diestien, and Scaldisien.

Among the more important contributions made to the Tertiary stratigraphy and paleontology of Italy was a work published in 1814 by Giovanni Brocchi on the Subappenine fossils. These were described and illustrated and a record was made of their exact occurrence within the different strata from which they were collected. Attention was called to the biological similarities of some of the species to those now living in the Mediterranean and also to certain forms from the Paris Basin. Other investigations by Omalius d'Halloy in Belgium and other parts of southern Europe and Germany presented evidence for future correlation of the Tertiary deposits from different parts of the continent.

Among the earlier publications dealing with fossils and rocks of Tertiary age was the work by Conybeare and Phillips in 1822 in which the sedimentary deposits in Great Britain above the Cretaceous were classified in ascending order as the Plastic Clay, London Clay, Freshwater Beds, and the Upper Marine Formation consisting of the Bagshot Sands and the Crag. This work, along with numerous others including the description of fossil mollusks by the Sowerbys, afforded material for a comparison of the British Tertiary fossils with those described by Deshayes in 1824–1837 from the Paris Basin, Italy, and other parts of Europe. Deshayes recognized an increase in the proportion of living species among the successive faunas from earliest to latest Tertiary. During this time Charles Lyell, who had traveled extensively in France, Italy, and other parts of Europe, studied the Tertiary outcrops and also the fossil collections that had accumulated in the museums and universities. Working independently, H. G. Bronn made detailed investigations of the Tertiary rocks and faunas of Italy and also observed the increase in the percentage of living species and genera in the younger beds. Lyell, after considerable association with Deshayes in Paris, correlated the deposits of France with those in the south of England and, influenced by the increasing percentage of living species from the base to top of the Tertiary, established new terms for the major divisions. In the third volume of his *Principles of Geology* published in 1833 he introduced the names Eocene, Miocene, Pliocene, and Recent. In 1846 the name Pleistocene was introduced by Forbes to include the uppermost Pliocene of Lyell and deposits of glacial origin. After 1850 the additional divisions of Paleocene and Oligocene were added by other workers.

Geological and paleontological research in eastern North America during the first half of the nineteenth century was carried on largely under the auspices of the newly established state geological surveys and by individuals associated with a few universities and academies of sciences. Ebenezer Emmons, after a study of the rocks in New York State, classified them in upward succession as the Crystalline complex, the Taconic system of greatly disturbed beds, the New York system, and the Red Beds. The New York system consisted of nearly horizontal beds of sandstones, shales, and limestones, which he subdivided into the Champlain, Ontario, Helderberg, and Erie groups. A report published by James Hall of the New York Survey in 1843 subdivided the New York system into twenty-nine groups. The Paleozoic rocks of Pennsylvania were investigated by H. D. and W. B. Rogers, who in 1843 described their composition, lithology, thickness, and geologic structure. The coal in the upper beds was considered as having been formed from peat bogs occurring on the surface of an extensive plain which from time to time suddenly passed slightly below and above the level of the sea. The Rogers recognized the folded character of the Appalachian Range and considered its deformation to have taken place after the deposition of the coal measures. In 1847 James D. Dana attributed the folding to horizontal compression of the strata as the result of the slow cooling and contraction of the earth's nucleus.

The foundations of Tertiary stratigraphy and invertebrate paleontology in North America were established by the investigations of T. A. Conrad with a series of contributions commencing in 1832 and continuing to and beyond 1850. The more important of his earlier papers included descriptions and illustrations of the Eocene shells of Alabama, the medial Tertiary fossils of the Atlantic Coast, and studies of fossils collected by W. P. Blake in California, as well as those obtained by the Wilkes Exploring Expedition near the mouth of the Columbia River at Astoria, Oregon. Many of these contributions were published in the *American Journal of Science,* the *Journal of Conchology,* and the *Proceedings of the Philadelphia Academy of Sciences.* The visit of Sir Charles Lyell to America in 1844 rendered possible a comparison of the Tertiary deposits with those of Europe.

Research and Publication Facilities Prior to 1850

The earlier contributions to paleontology and historical geology in Europe were largely by men who were sponsored and financed by those in control of state governments or by financially independent individuals interested in scientific work. After the private publication of William Smith's geological map of a part of England the value of geological work by the state became apparent. The Geological Survey of the United Kingdom was founded in 1835 under the direction of de La Beche and about the same time preparations were begun for a geological map of France. In North America the State Geological Survey of North Carolina was established in 1823, other states following this example, South Carolina in 1824, and Tennessee in 1831, while the Canadian Geological Survey was founded in 1841. The universities in Europe have always taken an important part in advancing the sciences of paleontology and historical geology and in training future investigators. Collections of fossils, together with library facilities, rendered possible the comparison of materials gathered from various parts of the world. Toward the middle of the nineteenth century geologists and paleontologists established professional organizations which provided scientific meetings, where the results of investigations could be presented and discussed, as well as facilities for publication. The Geological Society of London was organized in 1807 and the Palaeontographical Society of London in 1847. Important monographs on both invertebrate and vertebrate fossils began to appear in 1847 in the German publication *Palaeontographica.* The Geological Society of Germany was founded in 1849 and in it have appeared many important contributions to the geology and paleontology of Europe and other parts of the world.

Invertebrate Paleontology 1850–1950

At the beginning of the second half of the nineteenth century the theory of the immutability of species, together with the idea of special creation, had been strongly challenged by an increasing number of scientific investigators. Many important papers and monographs had been published with descriptions and illustrations of genera and species. The morphology of the hard parts of different groups of invertebrate organisms was now well known; also the facts connected with the occurrence of fossils in successive layers of sedimentary rocks. Information concerning their geographic distribution and their relation to changing lithologic facies caused many investigators to accept partially the new concept of mutability of species. Those who now did so no longer considered a species as confined to a single formation or interval of geologic time but held that certain species of a fauna might survive and continue to exist in the next succeeding set of strata. These concepts profoundly modified the ideas previously held by scientific men in the fields of paleontology, geology, and natural history.

Speculative concepts of the principles of evolution had been expressed before but were not generally supported by scientific facts. Paleontological research was now endeavoring to inquire into the nature of evolutionary processes based on a growing knowledge of the succession of faunas through geologic time. Charles Darwin began his investigation of the origin of species during this interval of change in scientific thought and in 1859 his monumental work on *The Origin of Species by Means of Natural Selection* appeared. The ideas expressed in this work appealed strongly to H. G. Bronn, who had already considered that transitional genera and species in a fauna of a given time interval might extend across the gap into the next succeeding interval. He translated Darwin's work into German and it immediately influenced the thought of those scientists on the Continent who were concerned with paleontological investigations. Darwin, in attempting to account for the method of action in the theory of evolution, placed emphasis on those factors involved in environment, including variations in climate, temperature, accessibility of food supplies, and means of protection from other organisms living in the same environment. He considered also how these factors singly or jointly might react favorably or unfavorably on each individual, depending on how each particular feature of the anatomy might respond. Morphological characters of a varietal nature were considered to influfluence the individual's response to the varying stimuli of the environment; thus those individuals with the most favorable variations would survive. This concept was designated as the law of natural selection. The principles of sexual selection were also included.

Before leaving for North America in 1847 Louis Agassiz had published the results of ten years of research on fossil fishes. Emphasis was laid on genealogy, including progressive morphological changes of certain parts of the skeleton as observed in different species and genera in passing from older to younger time intervals. Agassiz showed that information from the phylogenetic history could be of great value to geology for the systematic classification of sedimentary deposits. He also pointed out the correspondence of certain changes in the embryonic development of an individual to those exhibited in the phylogeny during geologic time. During the second half of the nineteenth century, as a lecturer in Harvard University, he inspired many of his students with the spirit of research and the inclination to search further for more detailed factors involved in the process of evolution as shown in fossil organisms.

The detailed morphological study necessary to yield sufficient data for expanding these principles of evolution of organic life during past geologic epochs required that the investigator devote special attention to the fossils of a single phylum or subdivision of it. Accordingly the more important advances made during the past one hundred years have been centered on the study of special groups, with particular attention to their geologic history. Many monographs dealing strictly with the biologic aspects of faunas were, and still are being, published but some of the more important, while contributing to the problems of evolution, lay special emphasis on stratigraphic problems.

The important advances made in the science of invertebrate paleontology during the past one hundred years may best be outlined by the consideration of each invertebrate phylum separately.

Protozoa: The foraminifera, which in most cases have chambered tests, in 1798 were included by Cuvier in the Mollusca but later, when studied microscopically by Dujardin in 1835, were found to contain protoplasm which was free to circulate throughout the chambers, thus establishing their unicellular structure. During the second quarter of the nineteenth century d'Orbigny devoted much time to a study of the Foraminifera and in 1826 made this group of organisms a special order, which he included in the class Cephalopoda. The order was divided into 52 genera and over 500 species based largely on the morphological differences of the wall and the shape of the test. He later accepted the interpretation of Dujardin that the Foraminifera were protozoans and in 1839 revised the earlier classification so as to consist of 6 orders and 64 genera. His final paper in 1852 grouped the genera into 7 orders, in which the growth and arrangement of chambers were of fundamental importance for classification. He still adhered to the concept of immutalibity of species.

The foraminiferal investigations initiated by d'Orbigny were continued by numerous paleontologists, and many classifications were devised, based on different criteria as the description of new genera and species appeared in a rapidly expanding literature. M. S. Schultze in 1854 proposed that all of the foraminiferal genera be included in a single order Testacea, which he separated from the rest of the unicellular organisms of the phylum Protozoa. The species were included under 10 families and 112 genera, all classified according to the shape of the test and arrangement of chambers. Williamson, who devoted special attention to a detailed study of the structure of the hard parts, concluded that the great differences shown in the structural characters rendered difficult any exact classification. He regarded these differences as due largely to variation and arranged into groups those genera which appeared to be closely related and grading into each other. A classification founded on the number, structure, and arrangement of chambers of the test, as well as the perforate or imperforate character of the wall, was proposed by A. E. Reuss in 1861. In addition, differences in the chemical and mineralogical composition were included. All of the species were grouped into 21 families and 109 genera.

H. B. Brady (1884), who studied the Recent foraminifera obtained by the "Challenger" Expedition, constructed a classification consisting of 10 families and 153 genera based largely on the texture, shape and structure of the test, aperture, and number and arrangement of the chambers. He was not in agreement with Reuss, who had included all arenaceous foraminifera in the imperforate groups, because some of the genera possess mural pores. The Astrorhizidae were considered by Neumayr (1887) as a primitive group and as the ancestors of the other foraminiferal families already established by Brady. On the basis of this interpretation Neumayr built up a phylogenetic classification based in part on the stratigraphic range of species and genera.

Ludwick Rhumbler (1899) considered that the evolutionary development of foraminifera during geological time involved morphological changes which would produce a strengthening of the test and that the uniserial forms would be more easily injured or destroyed than the coiled types. Accordingly, he regarded the former as ancestral to the more complexly coiled forms, a conclusion which is not entirely in agreement with the information concerning the occurrences in the fossil record.

The evolution of the foraminifera was discussed in an important publication by Henri Douville (1907). In this he considered that the composition of the test was dependent to a large extent on the differences of environment under which the animal lived, that the calcareous forms were descended from the arenaceous, and that those with uniserial tests represented a more advanced state of development than the coiled forms. At present the arenaceous types are not considered ancestral to the calcareous. The classifications presented by Cushman from 1927 to 1940 raised the number of families to 49, which Cushman believed were derived largely from coiled, nonseptate genera; he also thought that the calcareous group had arenaceous ancestors. His classification accepts many of the principles advocated by Douville. Galloway in 1933 criticized Cushman's classification, asserting that the latter had established too many families and subfamilies and that many of the genera had been placed in wrong families and in incorrect relationships between families. Galloway's classification and arrangement of families were based on his interpretation of the phylogenetic character of the different groups and determined from a consideration of comparative morphology, the stratigraphic range of the different assemblages of genera, and the biogenetic law. He considered the foraminifera as consisting of two broad groups, one of which evolved from the Allogromiidae, the other from *Endothyra*. The former constitutes a group of foraminifera with a single chamber and, because of its chitinous wall, is rarely preserved as a fossil. However, he considered it ancestral to the nonseptate calcareous and arenaceous forms, including the Miliolidae.

The most recent classification is by M. F. Glaessner, published in 1945. The order Foraminifera is divided into 7 superfamilies, 37 families, and 38 subfamilies. Glaessner concludes:

1. The non-septate forms are more primitive than the septate.
2. The higher, or septate, spirally coiled arenaceous foraminifera form a well-defined group.
3. The Fusulinidae are derived directly from Endothyridae.
4. The different lines of the porcellaneous foraminifera have a common origin in a coiled non-septate form.
5. The Polymorphinidae are derived from Legenidae but there is no clear evidence concerning the origin of this family.
6. The Cassidulinidae and Ellipsoidinidae (Pleurostomellidae) are related to the Buliminidae which can be traced back to a trochospiral ancestral form. Most of the other smaller calcareous perforate foraminifera are clearly derived from rotaloid (trochospiral) ancestors.
7. Most of the larger calcareous perforate foraminifera including *Siderolites*, *Orbitoides*, *Lepidocyclina*, *Miogypsina*, and probably the nummulites, developed from a number of different but closely inter-related small rotaloid (trochospiral) ancestors.

The ever-increasing demand for gas and petroleum products over large areas of the world intensified stratigraphic investigations and paleontologic research. Foraminifera began to play an important role in the determination of the geologic area of strata associated with the occurrence of oil. Thick deposits of shale with a wide areal geographic distribution often are nearly barren of diagnostic metazoan invertebrate fossils but are rich in foraminifera and other microscopic organisms. Because of their small size, well preserved faunas consisting of a vast number of individuals may be obtained from small samples of rock such as drill cores. The growing demand for scientifically trained investigators in micropaleontology soon led to the introduction of special courses in many universities where opportunity was available for instruction in this field. The larger oil companies began to add micropaleontologists to their geological staffs and some companies established special departments with well-equipped laboratories for handling this kind of work. Many important contributions to foraminiferal research have resulted from investigations carried on by those associated with the oil industry. Not only the universities of North America but those in other parts of the world as well have contributed to the description of new species and genera and their stratigraphic relationships. Increasing attention is being devoted to this kind of research by national and state surveys with the publication of many important papers and monographs concerned with foraminiferal faunas. Such investigations have been augmented by scientific and professional societies and academies throughout the world. Conspicuous among those in North Ameria are the Cushman Laboratory for Foraminiferal Research, the Paleontological Research Association and the Paleontological Society, and the Society of Economic Paleontologists and Mineralogists.

As the result of investigations during the past one hundred years there have been described about 4,000 species of Foraminifera distributed through nearly 300 genera. The practical application of micropaleontology has involved the use of species in local basins for deciphering the succession of strata as exposed at the surface and in the recognition of such beds under a deep covering of younger deposits as revealed in the cores obtained by drilling. Only a part of this detailed information has been available to those paleontologists concerned with the more purely scientific aspects of investigation, including the regional distribution, stratigraphic succession over wide areas, and ecological relationships. However, an increasing record of statistical data in recent years has made possible the publication of important papers dealing with an understanding of the ecology of assemblages, the influence of environmental changes in the composition of faunas from the study of living species, variation in species, and worldwide succession of faunal zones. From such research, modifications are being made in phylogenetic classification and in the evolution of different groups of foraminifera.

Porifera: In the early part of the nineteenth century there was uncertainty whether sponges were animals or plants. The group was investigated by Robert Grant of England, who in 1825 ascertained their affinity with the animal kingdom. Seventy-five species were described by Goldfuss (with G. Munster) in his *Petrefacta Germaniae* published in 1826, but the morphology of the group was still little known. Fossil sponges from the Upper Cretaceous of England were studied by Toulmin Smith in 1847–1848 with special attention to the structure of *Ventriculites,* which he considered related to the Bryozoa. In 1852 d'Orbigny classified the sponges as Amorphozoaires, dividing them into two orders: (1) Amphozoaires á squelette corné and (2) Amphozoaires á squelette testacé. The first order included living forms and the fossils belonging to the genus *Cliona;* the second order was divided into five families. The finer morphological characters of the skeleton were not considered, and his classification was based largely on external features. E. de Fromentel (1859) in his introduction to the study of fossil sponges—both living and fossil—considered the canal system, pores, osculum, and tubules for classification purposes. Sponges from the Jura Mountains were investigated by Étallon in 1859 and 1861, with special attention to the spicules, canal system, and the outer form, all of which he considered of importance for classification. Ferdinand Roemer (1860) studied the Silurian sponges of western Tennessee and defined the genera *Astylospongia, Palaeomanon,* and *Astraeospongia.* In 1864 F. A. Roemer published a monograph on the sponges of the North German Cretaceous, with the description of many species and an excellent account of the structure of the skeleton of the Hexactinellids and Lithistida. Sponges from the Miocene rocks of Oran were described in 1872 by A. Pomel, who developed a classification consisting of two broad groups, (1) Camptonspongiae and (2) Petrospongiae. The first, with two orders, was characterized by isolated spicules; in the second, with 239 genera, the spicules were arranged in a united framework. Wyville Thompson, who studied the sponges collected by the "Challenger" Expedition, was the first to point out a similarity of structure in the fossil *Ventriculites* to that in living siliceous sponges. In the last quarter of the nineteenth century considerable advance was made in the study of sponges as the result of the examination of thin sections under the microscope. By this method Sollas in 1877 compared several genera from the English Chalk with living hexactinellids and monactinellids. Similar studies by von Zittel (1877–1878) led him to consider that all sponges, both fossil and living, should be included in a single classification. Hinde, in the light of increasing knowledge of the morphology, presented a classification very close to that now in general use. It included the four orders Myxospongia, Ceratospongia, Silicispongia, and Calcispongia. A discussion of the advances made in the investigation of fossil and Recent sponges, along with a more advanced scheme of classification was given in a monograph by Rauff in 1893–1894. This grouping is used in the translation by Eastman (1913) of von Zittel's *Invertebrate Paleontology,* in which the sponges are placed in the phylum Coelenterata along with the corals but are included in the subphylum Porifera and in the class Spongiae. The four subclasses Myxospongiae, Ceratospongiae, Silicispongiae, and Calcispongiae are still recognized but the first two, because of their lack of imperishable hard parts, are not included in the textbook. The Silicispongiae are divided into four orders, the last two of which include the majority of fossil sponges. The Calcispongiae include two orders, Pharetrones and Sycones. The classification is based largely on differences in the character of spicules, whether single or united into a framework, thickness of walls, character of pores and tubes, and the osculum.

Monographs dealing with special groups of sponges have contributed greatly to the advances made during the past sixty years. Among the more important of these is the work on the *Dictyospongiae-Paleozoic Reticulate Sponges,* which was published by James Hall and J. M. Clarke (1898). These sponges are particularly abundant in the Devonian of New York State. In 1842 T. A. Conrad described and named *Hydnoceras tuberosum* and considered it a cephalopod. Lardner Vanuxem described *Uphantaenia chemungensis* as a marine plant. Another closely allied form was called *Dictyophyton,* revealing these authors' concept of its place in the classification. Many diverse forms were described before 1880 but the conditions of preservation made recognition of their real nature difficult. The internal and external casts of their bodies left distinct impressions of their spicular network. Similar fossils from Crawfordsville, Indiana, yielded more definite evidence and led to a recognition of their relationship to the living reticulate silicious sponges represented by *Euplectella aspergillum.*

A group of Cambrian sponges of the class Pleospongia were investigated in great detail by Vladimir J. Okulitch (1943). His classification is based on their morphology, affinities, and distribution. The first representatives of this class were described in 1861 by E. Billings of Canada as *Archaeocyathus* from the Lower Cambrian of Labrador. Okulitch's classification consists of 5 subclasses, 11 orders, 20 families, and 89 genera. Previous to the appearance of this work the Pleospongia were variously grouped with the Foraminifera, Sponges, or Corals. Okulitch concludes that they represent a separate class of the Porifera which became extinct in the Upper Cambrian, that there are no links between the Silicispongia and Calcispongia, and that they should be regarded "as independent branches having a common ancestor in the Pre-Cambrian."

Coelenterata: The Coelenterata is a phylum more advanced than the sponges and consists of a large number of extinct and living species. They are represented in the fossil record from the Cambrian to the Recent. At present they are usually divided into the following groups: Hydrozoa, Stromatoporoidea, Graptozoa, Scyphozoa, and Anthozoa. Many genera and species of corals, both living and fossil, were described in the first decades of the nineteenth century but the organization of their morphological features was not well known. Among the earlier authors were Lamarck, Ehrenberg, and Goldfuss. Thorough investigations of living corals were made by Milne-Edwards and Haime. These were followed by special studies of particular groups of fossil forms, with special attention to the morphology and structure of the polyps and the occurrence and distribution of fossil faunas through geologic time, culminating in the *Histoire naturelle des corallaires* (1857–1860). The classification of Milne-Edwards and Haime is based on the differences in the septa and the methods by which new ones are produced. The subdivisions are based on the number of tentacles.

During the middle of the nineteenth century many papers, largely of a descriptive nature, were published, among the more important of which were those by Reuss, Fromentel, Hall, and Duncan. Differences in the method by means of which new septa originated in the Paleozoic Tetracoralla as compared to those of the Hexacoralla and Octocoralla were described by Kunth in 1869–1870. Thin sections made from the calcareous skeletons were subjected to microscopic analysis. A similar method of study was used also by Pratz and Koch with accompanying illustrations in their published work. In 1896 Maria Ogilvie investigated fossil and living anthozoans and presented her interpretations of the phylogenetic relationships of the Tetracoralla and Hexacoralla. Moseley (1877) in a study of *Millepora* showed the relation of Stromatoporans to certain Hydrozoa which earlier had been considered Bryozoa. Nicholson's (1886–1892) important monograph on all known Stromatoporoids was published in the 'nineties and has been followed, with many modifications, by later authors.

The fossil Stromatoporoidea consist of large calcareous masses with great variation in structure and shape. Their structure, based largely on fossils from western Germany, has been investigated by M. Heinrich (1914), who divided these organisms into two groups dependent on the massive or nonmassive character of of the fibers. Those forms having a regular rectilinear arrangement of the fibers were placed in the massive group and those with an irregular vermiculate arrangement of the hollow-fibered skeletal structures in the nonmassive groups. The principal characters used in both groups for distinguishing genera include the amount of regularity and varying pattern of the skeletal mesh.

An important contribution to the Anthozoa was published in 1900 by T. W. Vaughan, with special emphasis on the general character and bathymetric distribution of Eocene and Oligocene genera and species in North America. He considered that the classification of corals was in a very unsatisfactory condition, that "no classification that will stand the test of thorough criticism has yet been proposed . . . [and that] past classifications were based on some particular features of the skeleton without reference to the whole structure and history of the organism." He pointed out that Duncan had based his grouping on a combination of general skeletal features and mode of growth but had not searched for those characters which were of phylogenetic importance.

The accumulated evidence that the Tetracoralla were confined to the Paleozoic and the Hexacoralla to later geologic time led P. E. Raymond to consider that the cooler climate of Permian time had brought about the extinction of that group largely because they had become specialized as lime-secreting organisms in relatively high-temperature seas. He also proposed the idea that the Hexacoralla originated from an "*Edwardsia*-like actinian" of the Paleozoic and became a lime-secreting organism as the temperatures lowered at the close of the Permian. Robinson suggested that certain forms classed as Tetracoralla occurring in the Mesozoic were probably Hexacoralla and that a number of Paleozoic genera referred to the Hexacoralla were Tetracoralla. This pointed to a sharp distinction in the time relations of these two groups. The paleozoic *Cyathaxonia* was suggested as a specialized organism which might have evolved into Mesozoic types, in which through assumption of an upright position the columella would change from an excentric to a central location.

The graptolites, which are abundant as colonies in black shales of the early Paleozoic where they are compressed in the rock layers like fossil leaves, occur as individual polyps attached to a central axis. They are important for distinguishing the geologic age of Ordovician and Silurian rocks and were placed by many early authors, including Nicholson and Lapworth, with the Hydrozoans. However, Neumayr held that they could not be placed with any of the known classes of animals. In 1931 E. O. Ulrich and R. Ruedemann, who had investigated the graptolites for many years, discussed the question whether they should be classed with the Hydrozoans or Bryozoans. Their objections to placing them with the Hydrozoans were based on the ground that the Hydrozoa contain no structures in common with graptolites, that they exhibit a different type of symmetry, and that the graptolites include "a considerable number of unnaturally associated fossil types." Ulrich and Ruedemann considered that the graptolites were more closely related to the Bryozoans because of the character of the sicula, the mode of budding from the sicula, the bilateral symmetrical thecae, and the similar habitus of the two groups. Recently R. Kozlowski (1948), in studying excellently preserved material from Lower Ordovician cherts in Poland, has concluded that the graptolites are closely related to the living Pterobranch *Rhabdopleura* of the phylum Hemichordata.

The fossil Medusae, which usually possess only a slight resemblance to living medusae, have been described in an important monograph by C. D. Walcott (1898). During the second half of the nineteenth century many species were figured and discussed by Beyrich, Haeckel, Ammon, and Nothorst.

Echinodermata: The accumulated information of 1850 concerning the morphology and classification of the phylum Echinodermata had resulted from investigations carried on in both Europe and North America. The Crinoidea were established as an independent group by J. S. Miller in 1821, the Blastoidea by Fleming in 1828 and the Cystoidea by von Buch in 1845. In 1848 Leuckart combined these under the class name Pelmatazoa and placed it along with other echinodern groups in the phylum Echinodermata. Important monographs by Goldfuss and Munster in 1826, Johannes Müller in 1841, Vaughn Thompson in 1836, Edward Forbes in 1848, and d'Orbigny in 1840–1860 emphasized the morphological details of genera and families along with the description and illustration of new species with attempts at broad classifications. From 1850 to 1950 a very extensive literature accumulated concerning the morphology and classification of echinoderms and the relationships of genera to their stratigraphic succession.

The earliest classifications of the Pelmatazoa were not founded on morphological principles, and many greatly differing forms were combined and placed in the same group. The Blastoids and Cystoids were placed by those immediately following J. S. Miller as a subordinate group under the Crinoids. Miller had divided the Crinoids into four groups, largely on the number and arrangement of the plates in the dorsal cup. Most investigators following Johannes Müller considered that all Paleozoic forms were distinct from later ones and it was not until the publication of Carpenter's work in the "Challenger" reports in 1884 on the stalked Crinoids that the morphological relations between the Mesozoic and Paleozoic forms became known. He held that the Paleozoic Crinoids differed from those of later age in the character of their irregular symmetry. Many new species and genera of Crinoids and Cystoids from Bohemia were described by J. Barrande between 1877 and 1899. In 1845 von Buch gave the Cystoidea equal rank with the Blastoidea and Crinoidea. Ferdinand Roemer in 1855 published an important memoir on the Cystoidea and Blastoidea and divided the former into three groups. Neumayr considered the Cystoidea, Blastoidea, and Crinoidea independent classes and believed that the two last were derived from the Cystoidea.

During the fourth quarter of the nineteenth century the Pelmatazoa were the subject of intensive investigation by North American paleontologists. Among the more noteworthy were F. B. Meek, A. H. Worthen, E. Billings, James Hall, Charles Wachsmuth, and Frank Springer. Under the auspices of the Geological Survey of Canada Billings, in 1869 and 1870, published contributions on the structure of these forms, with special attention to the position of the mouth in relation to the ambulacral system. He concluded that the pores in the rhombs of the Cystoidea were respiratory organs and the homologues of the tubular apparatus which underlies the ambulacra of the Blastoidea. He pointed out that *Eocystites* was the most primitive genus of the Cystoids, with an indefinite number of plates without any radial arrangement. He showed that the hydrospires of the Blastoidea were connected in pairs and had direct communication with the pinnulae. He thought that the mouth and anus combined represented the opening in the disk of Paleozoic Crinoids and that the grooves which pass from the center of the disk at the inner floor were conected with the ambulacral system and communicated through the arm openings with the arm grooves but did not enter the tegminal aperture. He considered that the food entered the body through the arm openings and was carried underneath the tegmen to a common oral center. Meek and Worthen added to these morphological studies, with attention to the ventral surface of the calyx, the plates, mouth, and anal openings.

In North America little attention had been given to the Crinoids until 1858 but by 1897 over 1,400 species had been described. Until the publication of the "Challenger" reports studies were confined largely to the abactinal side of the calyx and no attempt was made to homologize the plates of the tegmen of the different groups. The excellently preserved and abundant faunas of the late Paleozoic in the Mississippi Valley drew the attention of Wachsmuth and Springer, who, during the last quarter of the nineteenth and first quarter of the twentieth centuries, contributed many important papers and monographs on the Pelmatazoans. Among these was a three-volume work published in 1897 by the Museum of Comparative Zoology on *The North American Crinoidea Camerata*. Special consideration was given to morphological and phylogenetic characters, with an accompanying classification which is widely accepted at the present time. They point out "that the Crinoids were most intimately connected from the Silurian down to the present and only the Camerata, a highly specialized type, became extinct at the close of the Paleozoic." All American species of the Camerata known at that time were described in this monograph. They noted that the Crinoids, Blastoids, and Cystoids differ from other Echinoderms in being at one stage of life provided with a stem for attachment to other objects, thus living on their abactinal side in contrast to the other groups. Other important later contributions have been made by Jaekel on the phylogeny of the Pelmatazoa, by the revised textbooks of von Zittel, and by R. S. Bassler on the Edrioasteroidea.

Although many genera and species of Echinoids were described during the first half of the nineteenth century, the scientific approach to the investigation of the morphology and phylogeny began with the contributions made by Agassiz and Desor in 1840. These were followed during the next seventy-five years by the publications of Forbes, d'Orbigny, Wright, and Cotteau in Europe and by Hall, W. B. Clark, Twitchell, and Jackson in North America. The comprehensive monograph by Jackson in 1912 on the phylogeny of the Echini presents the information and interpretations made by numerous authors both in Europe and America, together with his own study of the morphology, development, and comparative anatomy of this class founded on the young and adult of fossil and living forms. His contribution includes a revision of the Paleozoic Echini and a systematic description of all known Paleozoic forms. He assumes that any scientific classification should be based on the totality of characters and not on single phases of the morphology. Emphasis is laid on the use of stages in development and a comparison of these with the characters of more or less closely associated types. He developed the idea of localized stages in development, the idea that, "throughout the life of the individual, stages may be found in definite parts that are comparable to the condition in the young and to adults of simpler types of the group." This principle was found applicable to such other groups as Crinoids, Corals, and Cephalopods and has been used by Hyatt, Beecher, Cushmann, Ruedemann, H. L. Clark, and many others. Jackson points out that senescence is well shown in Paleozoic Echini by the dropping out of columns of interambulacral plates at the dorsal portion of the test. He defines progressive types as "those which show in their development to maturity the addition of differential characters only . . ." without their later disappearance and points out that most Paleozoic Echini are of this type. Regressive types are considered to be those which show specialized characters in later development but lose these before old age so that the adult is simpler than its own young. Other characters discussed by Jackson are acceleration of development, parallelism, and variation.

The more important factors used by Jackson in considering the comparative morphology of the Echini were the form of the test, the pentameral system, the structure of the skeleton, the ambulacra and interambulacra of the corona, the spines, peristome, and occular and genital plates. His classification of the Echinoidea consists of 7 orders and 17 families.

After a critical study of plate structure, Sven Lovén in 1874 devised a nomenclature for referring to the ambulacra in terms of the Roman numerals I to V and the interambulacra by the Arabic numerals 1 to 5. He established the method of determining the bilateral symmetry of the test by the presence of the madreporite or the periproct.

Important contributions were made to the Mesozoic and Tertiary Echinoids in North America by W. B. Clark in 1893, W. B. Clark and M. W. Twitchell in 1915, W. S. W. Kew in 1920, and Grant and Hertlein in 1938. Cenozoic Echinoids have been described by P. M. Duncan from Australia and by Duncan and Sladen from the Western Sind of India. The papers by J. Lambert and P. Thiéry (1909–1925) are important for their taxonomic work on the Echinoidea.

Fossil starfish are not extensively used for purposes of geological correlation, yet they occur in rocks from the Ordovician to the present. Many papers have been written describing genera and species, among the more important of which are those of Sladen and Spencer from 1890 to 1908 on the British fossil Asteroidea, F. Schondorf from 1907 to 1913 on the German Paleozoic forms, and a monograph by Charles Schuchert published in 1915 on the Paleozoic Stelleroidea. In this volume there are recognized 45 genera and 110 species. Fifty-one of the species are from North America, 53 from Europe, and 6 from the southern hemisphere. This paper is of special importance for its presentation of the skeletal terminology of the Asteroidea.

Brachiopoda: The class name Brachiopoda was proposed in 1802 by Cuvier. A memoir by von Buch in 1834 contained a classification based largely on the characters of the hinge area. The character of the brachial appendages, the septum, the muscular impressions, and other internal structures were used by

King (1846) in the construction of a classification in which the Brachiopods were subdivided into 3 orders, 16 families, and 49 genera. The important monographs by Thomas Davidson published at intervals from 1851 to 1885 present an excellent analysis of the morphological characters of the hard parts of both fossil and living Brachiopods, along with a description of the soft parts by Richard Owen. The classification is in part the one used at the present time and was constructed with special attention to details of muscular scars, the hinge, the shell material, and, in some forms, the brachial system. Other important contributions during the past one hundred years have been made by J. Barrande (1879) on the Silurian faunas of central Bohemia, Waagen (1879–1895) on forms from the Salt Range in India, Rothpletz in 1886, James Hall, J. M. Clarke, C. E. Beecher, H. S. Williams, E. R. Cumings, P. E. Raymond, C. D. Walcott, F. L. Kitchin, Carl Diener, Charles Schuchert, G. A. Cooper, C. O. Dunbar, Hertlein and Grant, and numerous others.

The majority of the larger monographs and papers contain descriptions of new genera and species from particular areas or formations. Among these are studies on the Guadalupian faunas by G. H. Girty (1908), the Cambrian brachiopods by Walcott (1912), those of the Kutch Jurassic in India by Kitchin (1900), and the Tertiary forms by Sacco (1902). Other papers deal largely with problems of morphology and phylogeny of special groups or of the class as a whole. Important studies on the development and classification of stages of growth of brachiopod shells were published in 1891 and 1892 by C. E. Beecher, who applied the law of morphogenesis as earlier proposed by Hyatt. The principal factors used were those of growth and acceleration of development, of mechanical genesis, and geological sequences of genera and species. Special attention was devoted to the study of the embryonic shell or protegulum and its modifications resulting from acceleration, thus showing how the nepionic and neantologic characters are pushed forward and appear earlier in the history of the individual so as to become impressed on the early embryonic shell. As a result of special studies of the pedicle opening Beecher outlined the origin of the deltidium and deltidial plates and developed a classification of stages of growth and decline through the embryonic and larval stages.

E. R. Cumings (1903) published a paper on the morphogenesis of the post-embryonic stages of the genus *Platystrophia* in which he followed the principles used by Hyatt, Beecher, and Jackson. This was a critical study of the nepionic, neanic, ephebic, and gerontic stages of the genus with a general discussion of the history of the genus and the laws governing its evolution. Two important contributions, by Charles Schuchert and by Schuchert and Cooper, have added greatly to the knowledge of the brachiopods. The first paper (Schuchert, 1897) presents tables of species of North American brachiopods arranged by periods and with a classification consisting of 4 orders, 49 families and subfamilies of which 43 became differentiated in the Paleozoic and 30 were extinct before its close. Thirteen continued into the Mesozoic and 6 are represented by living species. The structural characters are given for each order and the classification is built upon morphologic and phylogenetic principles. The second paper (Schuchert and Cooper, 1932) is a detailed study of the suborders Orthoidea and Pentameridae. The authors consider that the division Orthoidea contains the primary stock from which all articulate brachiopods, including the order Telotremata, have arisen. The classification shows that for the genetic relationships use was made of all parts of the hard anatomy.

In the interval between 1910 and 1932 significant advances were made in the classification of certain Upper Paleozoic brachiopods, with emphasis on the internal structures as viewed under the microscope in thin section. In 1910 Ivor Thomas published an important memoir on the British Carboniferous Orthotetinae and in 1914 a memoir on the British Carboniferous Producti, in which a special terminology was introduced for the investigation of the shells of species which had been collectively grouped under the name *Productus*. As a result several species were separated from *Productus* and placed in four newly created genera. In 1910 Stoyanow placed the species *typica* with a vertical partition in the pedical valve in a new genus *Tschernyschewia*. G. S. Girty, also in 1910, described the species *elegans* with a transverse partition under the new genus *Diaphragmus*. However, a detailed study of the original material of *Productus productus* (Martin) by Muir-Wood in 1928 revealed that that species also possessed a transverse partition and, according to the rules of priority, *Diaphragmus* was placed in synonymy by Dunbar and Condra in 1932. The discovery made by Muir-Wood resulted in the elimination from the genus *Productus* of a vast number of species with vertical partitions and the erection of twenty-nine new genera and subgenera by Dunbar and Condra. The genus *Productus* in its restricted usage occurs only in the Lower Carboniferous. Other important contributions have been made by Stuart Weller (1914) and Th. Tschernyschew (1902).

Pelecypoda and Gastropoda: These organisms have become increasingly abundant in number of genera and species during the course of geologic time, reaching their acme during the Tertiary and Recent. They are thus important to the geologist concerned with the later geologic periods. The advances made in the science of conchology have been intricately associated with the investigations of fossil shells, although the classifications are based largely on the morphology of the soft parts. In general, paleontologists have adopted some of the broader groupings of families and subfamilies used by zoologists, but the descriptions of genera and species deal almost entirely with the morphological characters of the hard parts.

By the middle of the nineteenth century there had been described and illustrated a vast number of genera and species, both fossil and living, and to enumerate all the important authors would exceed the limited scope of this review. In the first half of the century the works of Lamarck on the Tertiary mollusks of the Paris Basin and the early work of Paul Deshayes (1824–1837) presented a classification and laid the foundation for further molluscan research in both Europe and America. Other contemporaneous investigators included the G. B. Sowerbys (father and son), Schlotheim, and Goldfuss. By the middle of the century many investigations were undertaken which resulted in monographic studies of special groups of mollusks as well as of faunas obtained from particular formations.

Among the important publications concerned with the morphology and classification of molluscan groups is that of P. Pelseneer (1906) which devotes special attention to the gills. These characters can be used only with living forms but the groupings of genera based on that kind of information compares well with other classifications founded on a study of the shell characters. In 1884

M. Neumayr investigated the hinge structure of bivalve shells and proposed a classification based on the morphological characters of the teeth on the hinge plate. H. Douville in 1912 grouped the Pelecypods on the basis of adaptive radiation into a system, proposing three branches depending on the mode of life to which the animal was accustomed. Investigations of both living and fossil mollusks by W. H. Dall brought about a classification of the Pelecypoda in which all characters of the shell were considered but with special emphasis on the details of the hinge plate. This grouping of families and genera was used in the English translation of von Zittel's *Handbuch der Palaeontologie* in 1895 and in 1913 (Eastman, 1913), a grouping which, with many modifications, is in general use at the present time. Other notable contributions to the morphology of special groups of Pelecypods and Gastropods are those of R. T. Jackson (1890) on the phylogeny of Pelecypods, F. Bernard (1895–1897) on the morphology of the pelecypod shell, Charles Deperet and F. Roman (1902) on Neogene Pectens, A. W. Grabau (1904) on the phylogeny of *Fusus* and its allies.

Several students of Mollusca have published reference books and monographs which are widely used by paleontologists engaged in the systematic description of fossil pelecypods and gastropods. Among these are H. and A. Adams in 1858, R. A. Phillipi in 1853, Tryon and Pilsbry's *Manual of Conchology* (1879–1898), J. C. Chenu in 1859, and F. A. Quenstedt in 1881. The many publications by M. Cossmann (1895–1925), including his thirteen-volume work *Essais de paléoconchologie compareé,* have been of fundamental importance for classification of gastropod genera. The "Gastropoda" section of the *Handbuch der Paläozoologie* (incomplete) by W. Wenz, 1938–1944, is an up-to-date and extremely valuable treatment of this class of Mollusca. The *Handbuch der systematischen Weichtierkunde,* by Thiele, is important for a comparison of the use of soft and hard parts of classification. One of the more recent contributions is *Tertiary Faunas,* by A. M. Davies (1934–1935). This work considers genera of Foraminifera, Echinoidea, Pelecypoda, Gastropoda, and some vertebrates characteristic of the Tertiary throughout the world and presents the morphological characters that distinguish genera, along with their stratigraphic range and geographical distribution. The early half of the twentieth century saw the publication of a very extensive literature by W. H. Dall and P. Bartsch on both fossil and living mollusca. These works deal with faunas of particular areas or with biologic groups.

A very extensive literature in which fossil mollusks are described deals with faunas of particular formations, with emphasis on stratigraphic problems. The importance of geology to the world-wide growth of the oil industry has stimulated research in stratigraphy and in the use of fossils to establish the time sequence of faunas. The result has been the publication of many papers with lists of faunas and the occasional description of new species.

Some of the more significant contributions of a purely scientific character during the past one hundred years are those of James Hall on the Paleozoic Mollusca of New York State, S. V. Wood on the Crag Mollusca of Great Britain (1851–1861), Morris and Lycett on the Great Oölite (1850–1863), J. Barrande on Silurian mollusks (1852–1899), Pictet and Campiche (1855–1872) on the Cretaceous Molluscs of Switzerland, and F. A. Quenstedt on the Jura in 1858. Papers dealing with the Mesozoic are those of A. Bittner (1895) on a revision of the Pelecypods of St. Cassian; W. H. Hudleston (1887–1896) on British

Jurassic Gastropods; F. Stoliczka (1868) on the Cretaceous Gastropods of Southern India; H. Wood (1899–1913) on the Cretaceous Pelecypoda of England; L. Waagen (1907) on Lamellibranchs from the Alpine region; A. P. Pavlow (1907) on the Aucellas of Russia; and F. L. Kitchin (1903) on the Jurassic Pelecypoda from the Kutch area of India. The late Miocene and Pliocene brackish and freshwater faunas of the Balkan Peninsula, Southern Russia, and the Caucasus have been studied by S. Brusina (1884), N. A. Andrussov from 1897 to 1912, and K. Krejci-Graf and Wenz (1931) who have directed attention to a succession of four nonmarine facies in a series of basins extending from Austria eastward into southern Russia and Asia Minor. In 1905, A. D. Archangelski described the Paleocene faunas in the Saratov area of eastern Russia and their relationship to faunas of similar age in Western Europe.

A few of the more significant contributions which have aided in making known the rich Tertiary faunas are those of E. Beyrich (1853–1856) on the North German Tertiary; C. L. F. von Sandberger (1858–1863) on Mollusca from the Mainz Basin; Hoernes and Auinger (1879–1891) on the Tertiary faunas of the Vienna Basin; S. V. Wood (1871–1877) on the Eocene Bivalves of England; K. Martin (1879–1880, 1891–1922, etc.) on the Tertiary Molluscs of the Dutch Indies; A. von Koenen on both the Cretaceous and Oligocene of Germany; M. Cossmann on the faunas of many formations in France; R. A. Philippi on the Tertiary of Chili; Nagao, Makiyama, and Hatai on the Tertiary Molluscs of Japan; A. Wrigley on the Eocene of England; and W. S. Slowkedwitsch on the Tertiary of northeastern Siberia. The faunas as described and illustrated in this last work closely resemble those of the middle and later Tertiary in Oregon and Washington.

The scientific contributions to molluscan paleontology of the western hemisphere during the past one hundred years have been exceedingly great and only a few of the more important can be listed. Among these are those of T. A. Conrad, who made known the occurrence of Tertiary Mollusca in both the eastern and western parts of North America; James Hall and J. M. Clarke on the Paleozoic mollusks of New York State and the upper Mississippi Valley; F. B. Meek on the Cretaceous mollusks of the Rocky Mountain region in 1876; C. A. White on nonmarine mollusks in 1883; E. O. Ulrich on the Silurian of eastern North America in 1897; T. W. Stanton on the Cretaceous; and W. H. Dall, H. A. Pilsbry, Julia Gardner, C. W. Cooke, Wendell P. Woodring, W. C. Mansfield, Katherine V. W. Palmer, W. B. Clark, G. D. Harris, and others in many papers on the Tertiary mollusks of the Atlantic and Gulf Coastal Plains and Caribbean regions during the last fifty years.

On the Pacific Coast the monumental works of W. M. Gabb and his associates from 1864 to 1869 made known the molluscan faunas of the Jurassic, Cretaceous, and Tertiary. Near the end of the nineteenth century important papers were contributed by T. W. Stanton and J. C. Merriam on the earliest Tertiary Martinez fauna and its relation to the uppermost Cretaceous. At the turn of the century an important paper on West Coast Cretaceous faunas, including pelecypods and gastropods, was published by F. M. Anderson under the auspices of the California Academy of Sciences. His later papers dealing with the same subject have recently been published by the Geological Society of America. Numerous papers appeared between 1915 and 1943 by B. L. Clark on the Tertiary mollusks of the Pacific Coast. Contemporaneously, the faunas of the Eocene were described by R. E. Dickerson (1914) and in 1925 the fauna of the type Tejon was described by F. M. Anderson and G. D. Hanna. In 1926 and 1930 two important monographs involving a detailed morphologic and systematic study of Gabb's types from California were published by Ralph Stewart. This work set the standard for more critical reviews of the generic nomenclature of fossil mollusks in many of the investigations which followed. A monograph dealing with a detailed systematic study of the mollusks of the Pliocene and Pleistocene of California was published by U. S. Grant IV and Hoyt Rodney Gale in 1931. Investigations of the species of particular genera such as *Acila, Nucula* and *Yoldia,* undertaken by H. G. Schenck at Stanford University during the second quarter of the century, pointed out the desirability of research on special generic groups. A very valuable catalogue was published by A. Myra Keen and Herdis Bentson in 1944 on all of the known Tertiary molluscan species in California.

Cephalopoda: The Cephalopods represented by both living and fossil groups were studied, described, and classified in different ways during the first half of the nineteenth century, but the vast literature which has accumulated concerning this class during the past one hundred years has revealed a fairly clear knowledge of their morphologic relationships. The living *Nautilus,* the cuttlefish, and Foraminifera were placed in the class Cephalopoda in 1798 by Cuvier and considered distinct from all other mollusks. In 1801 Lamarck noted the differences in the suture lines between *Ammonites* and *Nautilus* and in 1825 De Haan classified the known genera under three families—*Ammonitea, Goniatites,* and *Nautilea.* Owen in 1832, in a paper on the soft anatomy of the genus *Nautilus,* pointed out its relation to the Cephalopoda and divided that class into two orders, Tetrabranchiata and Dibranchiata, placing the living genus in the former. Von Buch, in papers published between 1829 and 1849, divided the Cephalopods into the Nautilidae and Ammonitidae largely on the position of the siphuncle, and separated the Ammontidae into three sections—*Goniatites, Ceratites,* and *Ammonites.* He introduced technical names for the different parts of the suture lines and used these, along with the varying shape and decoration of the shell, for the establishment of fourteen families. Observations made on the shells of many genera from the Paleozoic through to the end of the Mesozoic showed a progressive complication of the suture lines prophetic of future phylogenetic investigations. The new avenues of approach for the study of Cephalopods formed the groundwork for this type of research between 1850 and 1950 and resulted in the appearance of an extensive literature concerning the phylogenetic relationships of Paleozoic and Mesozoic genera.

Among the more important contributions to the study of the Cephalopoda at the opening of the second half of the last century were the works of F. A. Quenstedt on *Der Jura* in 1858 and *Die Ammoniten des Schwäbischen Jura* from 1885–1888. The monographs of Pictet and Campiche from 1858 to 1864 contain descriptions of the Cretaceous Cephalopods of Switzerland and those of J. Barrande (1852–1889) the Silurian Nautiloids of Bohemia. The morphological studies by Suess (1866) showed that, in addition to the details of the suture lines, the variations in the size of the chambers and the shape of the aperture were of importance in classification. With the use of these additional characters he introduced the new generic names *Phylloceras, Lytoceras,* and *Arcestes.* Contemporaneously in North America new methods were advocated by Alpheus Hyatt (1872) for the study of Cephalopods and by 1869 the earlier nomenclature of families was abandoned and a new system erected, which was founded largely on phylogenetic considerations. This early work was followed by numerous papers elaborating on the principles outlined, with the description of many sharply defined genera. Among the more important of Hyatt's papers was his "Genera of Fossil Cephalopods" in 1884 and the *Genesis of the Arietidae* in 1889. He introduced the method of study involving a detailed investigation of the successive whorls back to the initial chamber or protoconch and thus attempted to unravel the phylogenetic development in terms of the ontogenetic, thereby opening up a new line of research which has been followed by later students. These methods of attack were followed by M. Neumayr on the Ammonites of the Alps and North Germany from 1871 to 1881; Ed. Mojsisovics (1873–1876) on the Triassic of the Alps and on the Upper Triassic of the Himalayas in 1896; W. Waagen (1879–1895) on the Cephalopods of the Salt Range, India; and K. A. von Zittel on the Stramberger Beds (1868) and on the Tithonian of the Alpine region in 1870. Neumayr founded his classification of Cephalopods on a consideration of direct or close relationship of genera in the line of descent. Others who have added to the information concerning Cephalopods are Thomas Wright (1878–1885) on the Ammonites of the Lias of Great Britain; J. F. Pompeckj (1893–1896) on the Ammonites of Schwabia; A. Karpinsky (1889) on the Permian Ammonites of Russia; W. Branco (1880–1881) on the development and history of fossil Cephalopods; G. G. Gemmellaro (1887–1899, 1904) on the Ammonites of Sicily; and A. Fusini (1897) on the Liassic Ammonites of the Appenines.

From 1895 to 1919 C. Diener described the Ammonites of the Himalayan region and published papers on the environment, geographic distribution, sutures, and living chambers of Ammonites. In 1903 R. Hoernes discussed problems of ontogeny and phylogeny. The North German Ammonites were described in 1902 by A. von Koenen and the Jurassic Ammonites of France in 1910 by Dumortier. Papers by S. S. Buckman appeared from 1887 to 1900 on the Ammonites of the Lower Oolite of Great Britain and his monumental work on the Yorkshire Ammonites in 1909. The fine discrimination of species in this last work has been of fundamental importance to Jurassic stratigraphy. Notable contributions to the study of Ammonites during the past twenty-five years have been made by L. F. Spath in England and W. Kilian in France.

The significant publications of Hyatt in North America were followed by the contributions of numerous authors in the western hemisphere. In 1893 J. M. Clarke discussed the protoconch of *Orthoceras* and in 1897 the Lower Silurian Cephalopods of Minnesota. The Ordovician and Silurian Cephalopods were described by A. F. Foerste in 1921, and other papers dealt with the morphology of Paleozoic genera. These investigations were followed by the important papers of A. K. Miller on nautiloids and Paleozoic ammonites. The families of the Nautilidae, Hercoglossidae, and Aturiidae from the Pacific Coast Tertiary were discussed by H. G. Schenck in 1931. In addition to the early papers by Gabb on the Mesozoic Cephalopods of California and Oregon and those of Whiteaves (1876–1903) on the Cretaceous of British Columbia, there appeared in 1902 a monograph by F. M. Anderson in which many Upper Jurassic and Cretaceous species from the Coast Ranges were described. Later investigations by this same author on Ammonite faunas and their stratigraphic relationships were published by the Geological Society of America. Investigations on the Carboniferous and Triassic Ammonites of western North America and their relation to similar faunas in other parts of the world were published by J. P. Smith, of Stanford University, in 1903 and 1914. The scientific approach to the solution of his problems was patterned after that introduced by Hyatt. The Cretaceous Ammonites of the Upper Missouri region were described by F. B. Meek in 1876. Other important contributions on the Jurassic and Cretaceous Ammonites have been made by J. B. Reeside, Jr.

The Jurassic and Cretaceous Cephalopods of southern Texas and Mexico were studied and described by C. Burckhardt from 1906 to 1912 and the Permo-Carbonifierous Ammonites of the Glass Mountains by E. Böse in 1917. Similar paleontologic and stratigraphic studies in northern Mexico have been made by L. B. Kellum and R. W. Imlay during the past fifteen years. The short contributions made by d'Orbigny and von Buch during the first half of the past century to the invertebrate paleontology of South America were followed during the next one hundred years by many papers on the Mollusca, including Ammonites. The early investigations on the Cretaceous pointed to certain problems to be studied by later authors. Among these investigators were G. Steinmann, O. Wilckens, A. Ortmann, C. Behrendsen, H. von Ihering, W. Paulcke, T. W. Stanton, H. Gerth, P. Groeber, F. Krantz, A. F. Leanza, and E. Feruglio.

Arthropoda: The Trilobites, the most primitive group of this phylum, were abundant at the opening of the Cambrian, indicating that their ancestors probably lived in pre-Paleozoic seas, although their remains have not been discovered as yet. The name was introduced by Walch in 1771 (1768–1771, 3:120), and papers by J. W. Dalman in 1827, F. Quenstedt in 1837, Goldfuss in 1843, Burmeister in 1843, and H. F. Emmrich in 1845 proposed technical names for the different parts of the exoskeleton which were used for classification purposes. These include the number of thoracic segments, the character and position of the facial sutures, the shape and nature of the glabella, the presence or absence of eyes, structural differences, and the ability of the animal to enroll. In 1852 an important monograph by J. Barrande dealing with Silurian Trilobites appeared in which all the morphological characters of the exoskeleton were considered and certain phylogenetic relations pointed out. E. Billings in 1870 discovered appendages on the ventral side of the genus *Asaphus* in Silurian rocks and by 1950 similar fossil remains were obtained from *Triarthus, Neolenus, Calymene, Ceraurus, and Isotelus.* The monograph on British Trilobites by J. W. Salter and H. Woodward, published from 1867 to 1884, is important in that the authors take into consideration the dominant values in ontogeny as a basis for their classification. C. E. Beecher's paper on "Outlines of a Natural Classification of Trilobites," published in 1897, employs the phylogenetic concepts earlier offered by Hyatt and proposes a classification based on the morphogenesis of all parts of the carapace. He considered the Trilobites especially suitable for the application of the recapitulation theory because of their long history back to the opening of the Cambrian, their generalized structure, and the information available concerning their ontogeny. In an earlier paper on the larval stages of Trilobites he described the simple characters of the protapsis and the changes which it underwent during the development of the Trilobite. He showed that in the earlier Cambrian genera this stage is simple but that in the later, more complex genera by a process of acceleration certain characters have been advanced until they appear in the protapsis. He also pointed out that the ventral position of the free cheeks in the earliest larval stages of all except the highest Trilobites is evidence of low rank and for this group he proposed the name Hypoparia. Of the remaining Trilobites, those in which the free cheeks include the genal angles, he placed in the order Opisthoparia and those in which the sutures cut the lateral margins of the cephalon he designated Proparia. These three orders, with some additions and refinements, are in general use at the present time. Further evidence was presented to show that the eyes have migrated from the ventral side over the margin and then posteriorly across the cephalon to their adult position. Other changes were noted in the character of the glabella and the segments of the pleura. Beecher emphasized the erroneous earlier interpretations of the Trilobites as closely related to the living *Limulus*. They lack the operculum of the *Limulus* and possess primitive crustacean affinities in their protonauplius larval form, slender jointed antennules, the hypostoma and metastoma, five pairs of cephalic appendages, and the biramel character of the limbs. H. M. Bernard in his paper on the systematic position of the Trilobites in 1895 concluded that the crustaceans originated by the bending under to the ventral side of the anterior segments of an ancestral carnivorous annellid. Other significant papers have been published by C. D. Walcott on Cambrian Trilobites from 1881 to 1916, in which many new species have been described and illustrated. One of these in 1911 is devoted to a discussion of the Cambrian species of China.

The Eurypteriids of the Middle Paleozoic were studied by several authors in Europe and North America. F. Roemer in 1848 pointed out their relationship to the living *Limulus*. Other contributions dealing with this group are those of J. M. Clarke and R. Ruedemann, who in 1912 described the forms from New York State. The Ostracods, because of their importance in stratigraphic studies, have been investigated by C. I. Alexander (1933), and by R. S. Bassler and B. Kellett (1934), and many others. The fossil Decapods from both the east and west coasts of North America and Central America were described by M. J. Rathbun from 1918 to 1935.

Fossil insects occur in certain rocks where conditions for preservation were favorable and were described about one hundred years ago by E. F. Germar from Carboniferous formations near Halle, Germany, and by C. Brongniart from rocks of similar age at Commentry. The Lithographic Shales at Solenhofen also have furnished well preserved fossils, which were described by Meunier, Oppenheim, and Munster. S. H. Scudder in 1879 published an important paper on Paleozoic cockroaches and later (1886) an index to the known fossil insects of the world. In 1900 he described the insects of the Florissant shales of Colorado. Other important contributions during the past fifty years include a review of American Paleozoic insects by A. Handlirsch in 1906, a monograph by Petrunkevitch (1913) on terrestrial Paleozoic Arachnida of North America, and numerous papers by R. J. Tillyard, including his contribution (1923–1934) on the evolution of the class Insecta.

Sponsors of Research and Publication

During the past one hundred years research and publication of results have been carried on largely by technically trained people associated with national and state surveys, academies of science, organizations with funds available for special problems, and by the geological and paleontological staffs of universities in all parts of the world. The past three decades have witnessed the growing application of earth science to problems connected with the search for oil and gas. As a result, extensive funds have been available for world-wide research and in many instances for the publication of important scientific contributions.

The national and state geological surveys were established for the purpose of making known information concerning the natural resources in the rocks and the nature of the problems for their utilization. Many of these organizations have devoted their energies to the investigation and publication of problems connected with the direct application of geology and paleontology to the development of mining in its broadest sense. Others have considered the furtherance of research associated with the more purely scientific phases of paleontology as an important function. A large number of these organizations were founded before 1850.

Historical Geology 1850–1950

Pre-Cambrian time: Rocks of pre-Cambrian age have a wide areal distribution involving perhaps twenty per cent of the continents and presumably underlie as a basement complex all the Paleozoic and later formations. Since 1850 they have been studied extensively in eastern Canada and in the area of the Great Lakes. Over wide areas these rocks have been divided into two broad groups or systems, which are separated by a profound unconformity. The lower division usually consists of granites, gneisses, and highly metamorphosed sedimentary rocks and volcanic products: the upper of metamorphosesd and unmetamorphosed rocks, including slates, quartzites, graywackes, schists, gneisses, and eruptive rocks. Such materials are well exposed and have been studied in detail by many authors in northern Scotland and described as the lower, or Lewisian, and the upper, or Torridonian, systems. Gümbel proposed a similar twofold division for the basement rocks in Bavaria and Bohemia and, as in North America, referred to the lower series of gneisses and granite as Archaean and the upper gneisses, schists, limestones, and shales as Algonkian. A similar classification was adopted in 1905 by a committee of thirty-five geologists under the direction of Michel Lévy for the geological map of France. The pre-Paleozoic rocks of Scandinavia have a wide areal distribution and, after investigation by Tornebohm, were divided into two series, as in Great Britain. Sederholm in 1907 described an upper, fourfold division of metamorphosed sedimentary rocks as Algonkian; unconformably beneath these were a lower series of granites and gneisses and an upper one of metamorphosed sedimentary rocks. The investigations of von Richthofen in China, followed by those of Bailey Willis and Eliot Blackwelder in 1907, led to a classification somewhat similar to that in the Great Lakes area. In a general way the pre-Cambrian rocks of Western Australia, Africa south of the Sahara, northeastern South America, India, Siberia, and Russia have a similar representation. Certain of the lower formations in Russia have an age of 1,852,000 years, as indicated by the study of radioactive distintegration products.

Investigations of the rocks along the St. Lawrence River Valley in 1843 by Sir William Logan, the first director of the Geological Survey of Canada, resulted in the subdivision and differentiation of the pre-Cambrian and the grouping of the granites and gneisses under the term Laurentian. Later his studies were extended into the area north of Lake Huron where he found a series of slates, quartzites, and conglomerates containing pebbles derived from the underlying Laurentian granites. He called these rocks Huronian, from their occurrence on the northeast side of the lake. He recognized a third series of still younger volcanic rocks containing copper and interbeded sedimentary rocks which he considered as a part of the Huronian. Later, in 1876, these rocks were named Keweenawan by Brooks. These studies were followed by detailed investigations of particular areas by Dawson, Bell, Coleman, Collins, and Barlow in Canada and by Van Hise, Leith, Irving, Lawson, Pettijohn, and many others in the United States. The areas involved included Newfoundland, Nova Scotia, New England, parts of the Appalachian region, Montana, the Grand Canyon area in Arizona, the Llano area of Texas, and many parts of the Cordilleran region.

The term Archaean system was defined by Dana in 1872 so as to apply to all pre-Cambrian rocks. Extensive outcrops of greenstones and green schists in the Lake of the Woods area in Canada, which overlie the younger intrusive Laurentian granites earlier described by Logan, were studied by A. C. Lawson in 1885 and named the Keewatin series. Lawson also defined the Coutchiching series, consisting of mica schists that were originally sediments, well exposed in the Rainy Lake area and believed that these rocks underlay the Keewatin. He later observed that a thick accumulation of slaty shales, with a basal conglomerate consisting of boulders derived from the Laurentian granites, rested upon the old intrusive rocks and that these in turn were invaded by a later granite. Lawson named these sedimentary rocks the Seine River series and applied the term "Algoman granite" to the later intrusives. Other rocks of similar age in another region were named the Timiskaming series. Thus there were recognized two periods of batholithic intrusion prior to the deposition of the Huronian system. Collins, in 1922, determined that a third intrusive interval occurred after the accumulation of the Keweenawan volcanics and was accompanied by strong mountain-making movements which brought pre-Cambrian time to a close.

The downwarping of an extensive peneplain carved out of the Algoman Mountains formed an area for the deposition of the Huronian sediments which have been defined as the Bruce, Cobalt, and Animikie formations. North of Lake Huron the lower beds consist of nearly twenty thousand feet of coarse sandstones and conglomerates containing striated boulders, which were interpreted by A. P. Coleman in 1908 as a tillite indicative of an early ice age. The Animikie series was named in 1873 by T. S. Hunt, of the Canadian Geological Survey, and consists of metamorphosed and unmetamorphosed rocks, including slates, quartzites, graywackes, schists, and eruptive rocks. Originally these were thought to be a part of the Keweenawan series but later this series was found to be unconformable on the Animikie. Because of the great differences of opinion concerning the classification of these rocks a committee of geologists was appointed to study them and in 1904 placed the Animikie in the Upper Huronian and unconforably beneath the Keweenawan.

In his earlier work along the north side of the St. Lawrence Valley Logan described a very thick series of metamorphosed limestone and schist, which he named the Grenville series. These sediments contain thick beds of graphite, which are considered to have been derived from some very early organic source.

Pre-Cambrian rocks are well exposed in the gorge of the Grand Canyon of the Colorado River and were first made known by Powell in 1875. The Upper pre-Cambrian sandstones, shales, and limestones were described as being 10,000 feet thick and were named the Grand Canyon series. They are separated by a profound unconformity from the Cambrian above and also from the older hornblende and micaceous schists and gneisses below, which later, in 1886, were named the Vishnu schist by Walcott. Pre-Cambrian rocks similar to those in the Grand Canyon have been described from the area of the Little Belt Mountains in Montana in the reports of the Hayden Survey in 1872–1873, by Davis in 1886 from the headwaters of Belt Creek, by Peale in 1893–1897, by Weed and Pirsson in 1896, and by Weed in 1899 from the Fort Benton and Little Belt Mountains quadrangles. These rocks consist of a lower group of greatly metamorphosed rocks, separated by a marked unconformity from the upper Algonkian sediments, which were named the Belt series. The latter are unconformable beneath the Cambrian.

The fossil remains of algae, worm burrows, and sponges have been found in the Algonkian rocks but the only evidence of life in the older groups are carbonaceous slates and graphite. Accordingly, the older rocks have been referred to as Archaeozoic and the younger as Proterozoic, although the United States Geological Survey uses the term Proterozoic for all pre-Cambrian rocks, with the two subdivisions Archaean and Algonkian.

Recently, Rankama (1948) has shown that the C^{12}/C^{13} ratios in a number of pre-Cambrian carbon-bearing rocks of Finland are similar to the ratios present in many organic substances and not similar to the ratios in inorganic accumulations of carbon. It thus appears that the carbon in these rocks was accumulated by organisms. Rankama concludes that the problematical *Corycium enigmaticum* Sederholm from the late Archaean of Finland is a real fossil, probably a primitive alga. This method appears to offer much promise for the determination of the remains of organisms in pre-Cambrian sedimentary rocks.

Lower Paleozoic: The controversy concerning the classification of the lower Paleozoic rocks of Great Britain during the first half of the last century continued until 1879 when Lapworth proposed the term Ordovician system for beds previously called Lower Silurian and Upper Cambrian. Thus the lower Paleozoic rocks were classed as three independent systems under the names Cambrian, Ordovician, and Silurian. Investigations carried on by the Geological Survey of Great Britain during the past one hundred years show that the Cambrian rocks of the British Isles consist of more than 12,000 feet of sandstones and shale which have been strongly folded, faulted, and in places partially metamorphosed. The Ordovician formations are best represented in Wales and western England.

Important investigations on the lower Paleozoic strata of Bohemia were made by Joachim Barrande and published in twenty-two volumes from 1846 to 1883.

The Middle Cambrian section is one of the most complete in Europe and its abundant fauna is well preserved. The succession of Ordovician beds in the Bohemian Basin is representative of the rocks of that system for Europe, and its fossils have been fully described by Barrande. He also made known the richly fossiliferous Silurian limestones of this area, including with them strata which later were considered by Emmanuel Kayser and others to be Devonian.

Lower Paleozoic rocks have a wide distribution in the Baltic region and eastward through northern Russia. The most complete succession of the Silurian formations in Europe occurs on the island of Gotland, where limestones predominate. The Silurian rocks of Sweden and their faunas were studied by Angelin in 1854 and, on the basis of Trilobite genera, were divided into seven stages. The Ordovician system in Sweden, as in many parts of the world, is in part composed of shales rich in graptolites, which have been studied by numerous paleontologists and correlated with the similar succession in Great Britain.

The major subdivisions of the early Paleozoic rocks of eastern North America were studied by Ebenezer Emmons prior to 1850 and in the following years important supplementary contributions were made by James Hall, J. D. Dana, H. D. Rogers, William Mather, C. D. Walcott, and many others. The final report of Rogers in 1858 on the geology of Pennsylvania adopted in part the classification earlier proposed in New York State and suggested the idea of the Appalachian trough as a basin of deposition, with a land mass, lying to the east and partly beyond the present coast, as a source of the Paleozoic sediments. The Lower Paleozoic rocks in western Massachusetts and eastern New York, like those in Wales, have been strongly folded, faulted, and partially metamorphosed; they rest on gneiss, so that the problem of their classification was for many years involved in controversy. Emmons thought these rocks were older than the Upper Cambrian Potsdam sandstone of northern New York and proposed for them the name Taconic system. Numerous investigations during the past one hundred years resulted in an explanation of the Taconic problem: namely, that moderate uplift during the Ordovician became accentuated near its close, with folding and overthrusting, and a chain of mountains extending from Newfoundland southward to New Jersey was produced. This event has been termed the Taconic disturbance; in consequence of it the Silurian formations rest unconformably upon the beveled edges of the older rocks. The effect of this disturbance diminished toward the west, where the lower Paleozoic strata are relatively horizontal.

The widespread lower Paleozoic formations in the Mississippi Valley and northern Gulf States areas were under investigation by the newly organized state geological surveys during the middle and late nineteenth century. Also, because of the relation of these rocks to the occurrence of oil and gas, particular areas have been studied in great detail during the past fifty years.

The name Cordilleran trough has been applied to an area in the Great Basin region extending from Arizona northward into Canada, which during the Paleozoic was at times a basin of deposition for great thicknesses of marine Paleozoic rocks. Numerous studies by the U. S. Geological Survey of areas containing mineral deposits have yielded stratigraphic and paleontologic information concerning Paleozoic strata and, although different names have been applied to widely separated stratigraphic sequences, a satisfactory correlation of beds is gradually being arrived at. The important monographs on the Cambrian faunas from the Canadian Rockies in Alberta by Walcott have made possible the division of that system into three series which serve as a standard for comparison with other areas.

Surveys made by the geological surveys of Russia and India have shown the presence of extensive areas of early Paleozoic sedimentary marine rocks in northern Asia southward into China and also the transgression of the Indian Ocean over parts of western India. Recent investigations show that rocks of early Paleozoic age occur across parts of New Zealand and Australia, in northern Africa, and in the central and western parts of South America.

Upper Paleozoic: The Devonian of Great Britain is represented by the Old Red Standstone, which had been made known through the writings of Hugh Miller prior to 1850. When it was realized that these rocks occupied a stratigraphic position between the marine fossiliferous beds of the Cambrian-Silurian and the Carboniferous of Devonshire and Cornwall, they were designated in 1837 as the Devonian system by Sedgwick and Murchison. Since 1850 they have been the subject of many detailed studies by British geologists and now are recognized as of flood-plain and eolian origin. The most complete Devonian sections from both a stratigraphic and faunal standpoint occur in the Rhineland and Eifel areas of western Germany. During the past one hundred years many important contributions have been made to the Devonian rocks and faunas in Russia, central Asia, and South America. In southwestern Australia Devonian rocks consisting of shales and sandstones are reported to have a thickness of nearly 25,000 feet.

By 1850 the areal distribution and broad lines of classification of Carboniferous rocks were fairly well known. During the past one hundred years many monographs have appeared with descriptions of the faunas and floras and many modifications of stratigraphic classification. In most parts of Europe these rocks have been and still are termed Lower and Upper Carboniferous in contrast to the Mississippian and Pennsylvanian systems of North America. The Carboniferous of Germany has been subdivided by Lottner (1868), by H. B. Geinitz (1856), and by F. von Roemer (1870). The Lower Carboniferous beds of Western Europe consist largely of fossiliferous limestone, in contrast to carboniferous sandstone and shale in the Upper. Eastward into Asia limestones have been found to prevail.

The association of coal, oil, and gas in rocks of Upper Paleozoic age in eastern and central North America has resulted in detailed investigations of these formations by State and Federal surveys. The areal and structural geologic maps of large areas of the United States have made known the lithology, thickness, and structure of the Devonian, Carboniferous, and Permian rocks and the classification of their subdivisions. The Carboniferous system has been recognized by the U. S. Geological Survey, with the Mississippian and Pennsylvanian as subsystems. These investigations point out the contrast between the strongly folded and faulted beds of the Appalachian area and the slightly tilted strata of the central part of the continent and also with the faultblock structures of the Cordilleran region.

A twofold series of uppermost Paleozoic rocks occurs in northern Germany between the Carboniferous and the overlying Triassic beds. The lower part of this series consists of red standstones, called the Rothliegendes, and an upper magnesian limestone known as the Zechstein. Resting on the red sandstone at the basis of the Zechstein are black copper-bearing shales, the Kupferschiefer. The Zechstein also contains deposits of potash salts. Because of the economic importance of these materials these rocks were studied in detail in the early part of the last century. Beds of red conglomerate and magnesian limestone in Devonshire, England, were considered by Conybeare and Phillips to be equivalent to the Rothliegendes and Zechstein of Germany.

Just before the middle of the last century Murchison, de Verneuil, and Keyserling examined the thick series of marls, sandstones, and limestones which rest on Upper Carboniferous beds in the west flanks of the Ural Mountains and proposed the name Permian for this system, a term which was immediately adopted in western Europe. In 1874 Karpinsky described beds with a transitional fauna between Upper Carboniferous and Permian and designated them the Artinskian stage. These faunas are known to have a wide distribution from the Arctic Ocean to the Caspian Sea. A complex of Permian and Triassic continental beds occurs in Central and Southern India; these have been studied by W. T. Blanford, of the Indian Geological Survey, and named the Gondwana system by Medlicott. These beds have yielded an important fossil flora, including the genus *Glossopteris,* and many fossil reptiles. The fossils of this series are important because of their widespread occurrence in Australia, Brazil, and South and East Africa and have been used as partial evidence for the proposed continental connections called Gondwanaland. The concept of Gondwanaland has been opposed by many geologists and modified by others, notably by Schuchert in his paper on Gondwanaland bridges.

Evidence for glaciation during the Upper Carboniferous and Lower Permian occurs in South Africa, India, Australia, Brazil, Uruguay, Bolivia, and the Falkland Islands. The base of the Permian in Central India has been described as consisting of nearly two thousand feet of an old tillite, resting on the striated surface of older beds. These grade upward into sandstones and conglomerates containing *Glossopteris.* A similar record has been noted by E. H. Schwarz in South Africa, where the Dwyka tillite at the base of the Permian rests on a polished and striated surface, with evidence that the movement of the ice was southward away from the equator. In Australia, T. W. David reports that the tillite lies on Lower Carboniferous and older rocks and is overlain by coal-bearing sandstones carrying the *Glossopteris* flora. Largely because of differences of opinion concerning the boundary between the Carboniferous and Permian, many European and South African authors have tended to date the late Paleozoic glaciation as Upper Carboniferous. In 1928 Schuchert, after a review of the whole Permian problem, concluded that glaciation took place in Middle, and probably late Middle, Permian. He interpreted the climatic change as the result of the Hercynian orogeny which began in early Carboniferous time and continued periodically through the Upper Carboniferous into Permian time. The Australian geologists T. W. David and C. A. Sussmilch disagreed with Schuchert's interpretation and in their reply in 1931 gave evidence of six glacial stages, the first two of which were in mid-Carboniferous time, the third in Upper Carboniferous, the fourth in the Lower Permian, and the last two near the top of the Lower Permian. Later studies by A. C. Seward indicate that in Australia glaciation began in the Lower Carboniferous, continued into the Upper, and was accentuated in the Permian. In Kashmir the *Gangamopteris* flora is interbedded with strata equivalent to the *Productus* limestone. Knowlton considered that this flora originated either in Australia or Antarctica and, with the advance of the ice age, was dispersed northward throughout the southern hemisphere but was prevented from reaching the northern areas by the transverse sea which connected Tethys Basin with the Caribbean Sea and also by the prevailing aridity of northern lands.

Prior to 1900 the term Permo-Carboniferous was used widely in North America for sediments now referred to in part as Permian; as early as 1859 it was employed by Meek and Hayden for deposits in Kansas. In 1917 J. A. Udden made known in the Marathon area of western Texas a section of 6,000 feet of dolomites and limestone deposited during the Permian in a sea which occupied large areas of Texas, Kansas, and Oklahoma. This sea was limited on the west by the ancestral Rocky Mountains and on the southeast by the Llanorian uplift. From these lands and from the Arbuckle and Wichita uplifts came the sediments of this age, which are to a considerable extent red beds. Important contributions have been made to the study of these formations by Philip King, of the U. S. Geological Survey. In eastern North America the Paleozoic Appalachian trough was drained and the thick accumulation of sediments folded, faulted, and elevated into the Appalachian Mountains at this time.

Triassic: The threefold classification of Triassic rocks of central Germany as the Bunter sandstone, Muschelkalk, and Keuper had been established prior to 1850, largely through the investigations of Alberti. Later each of these divisions was subdivided into groups with names based on local variations of lithology. The middle marine Muschelkalk member decreases in thickness westward and in England its equivalent, together with the Bunter and Keuper, forms a sequence of continental sandstones, shales, conglomerates, and local beds of gypsum and rock salt, which were named the New Red Sandstone. The north German Triassic became the standard for comparison with the Alpine areas during the second half of the last century.

The threefold division in Germany is not characteristic of the Alpine region, where folded and faulted fossiliferous marine limestones, dolomites, and shales form rugged outcrops extending from Austria westward to the Jura Mountains. Several important monographs on the stratigraphy and faunas of these rocks had been published before the middle of the past century by Lill, H. G. Bronn, Klipstein, Emmrich, Hauer, and von Buch. As a result a partial correlation of the Alpine Triassic with that of northern Germany was made by a comparison of distinctive faunal assemblages. In 1858 F. Hauer, of the Austrian Geological Survey, divided the Triassic succession in the Venetian Alps into seven groups on the basis of the paleontological sequence. Von Richthofen in 1860 published a work on the Triassic of the South Tyrol, with a full description of the areal distribution, lithology, and tectonic structure of the different formations, and made the suggestion that the limestones of the Southern Alps had been formed by the slow subsidence of reef-building corals. Investigations of the Bavarian Alps by Oppel in 1859 and Gümbel in 1861 led to the recognition of the Dachstein limestone and the Kossen formation as the Rhaetic group of the uppermost Triassic. Gümbel, while director of the Bavarian Geological Survey, studied the Alpine region in great detail. He proposed the name Vindelic Chain for a former mountain range north of the present Alps, extending from north Bavaria westward to the plateau of central France, and accounted in this way for the differences in lithology of the Alpine and Extra-Alpine Triassic.

The investigations of E. von Mojsisovics in Austria between 1866 and 1896 emphasized the paleontologic basis for the classification of the Triassic massive limestones in contrast to the earlier divisions founded on lithology. The Triassic rocks of the Himalayas and Salt Ranges of India were studied by von Mojsisovics, Diener, and Waagen under the auspices of the Geological Survey of India and have been classified largely on the basis of the divisions established in the Alps. An evaluation of the Permo-Triassic horizons, including that containing the Djulfa fauna in Armenia, has been described by A. Stoyanow. L. F. Spath, in his monograph on the Ammonoidea of the Trias in 1934, has also contributed greatly to the discussion of these problems.

The Triassic rocks of eastern North America, extending from Nova Scotia into South Carolina, consist of continental red beds corresponding to the Keuper series of Germany and were named the Newark series. These sediments, ranging from 10,000 to 20,000 feet thick, along with basic lavas, accumulated in downfaulted troughs and were derived from the erosion of the recently uplifted Appalachian Mountains.

The Triassic continental beds of the Cordilleran basins of western North America were studied for nearly one hundred years by the United States exploring expeditions and later by the U. S. Geological Survey. They consist of colored shales, sands, and conglomerates, which have been named the Moenkopi, Shinarump, and Chinle formations. Marine members interfinger with the Moenkopi formation toward the west and in California and Nevada attain thicknesses as great as 20,000 feet. These deposits contain rich ammonite faunas, which were described by J. P. Smith and Alpheus Hyatt in 1905 and by J. P. Smith in 1927. The relation of these faunas to those of the Himalayas and Alps made possible an interpretation of seaway connections which during the Lower Triassic connected the Great Basin sea with the Arctic to the north and also with Tethys Basin, as pointed out by Smith. Later the connections were thought to be with the Mediterranean through the Central American portal and a mid-Atlantic archipelago. Again this avenue was closed and a Pacific boreal passage opened. The Upper Triassic faunas of western North America indicate that the connection was once more with the Mediterranean except at the end of the period when boreal faunas again came down from the Arctic.

Jurassic: The contributions of William Smith, together with those of Conybeare and Phillips, made the Jurassic succession in England well known by the middle of the past century. It was classified as the Lias and the Lower, Middle, and Upper Oolite. The early work of Humboldt, Brongniart, Merian, Thurmann, Dufrenoy, and Élie de Beaumont outlined the general features of the Jurassic rocks of Switzerland, France, and south Germany. Those of south Germany were divided into Black, Brown, and White Jura by von Buch, who laid the foundations for the important contributions of F. A. Quenstedt. In these the three main groups were each subdivided into six subgroups and an important section was established in the Schwabian Alps which was extensively used as a standard for correlation.

The monumental work *Paléontologie française*, by d'Orbigny (1840–1860) which was partly complete in 1856, presented a classification of the Jurassic rocks and faunas of France, but d'Orbigny still considered that each stage contained a specially created fauna, distinct from all others below and above. After a study of the Jurassic in France and England the detailed investigations of Albert Oppel, published in 1858, led to the introduction of the term "zones" for time-stratigraphic units based on the occurrence of certain species which were absent in beds above and below. This work was of fundamental importance for future stratigraphic investigations. The lithologic similarities of the uppermost Jurassic and lowermost Cretaceous rocks in the Alps made it difficult to separate them. Oppel used the term "Tithonian" for the uppermost Jurassic limestones and shales in the northern Alps; and the characteristic Tithonian fauna has made possible the correlation of beds with similar faunas in distant parts of the world. The Upper Jurassic faunas in England and Germany are not everywhere characterized by Alpine species; the upper part of the Tithonian group is now recognized as equivalent to the Portland Purbeck beds, the lower to the Upper Kimmeridgian.

The Jurassic rocks of both northern and southern Asia are rich in fossils, which have been compared in important monographs by Waagen, Kitchin, and Noetling, to both the Alpine and northern European faunas. A nearly complete sequence of European faunal zones known in the Jurassic rocks of the Andean trough of South America have been studied by Bodenbender, Steur, Burckhardt, Gerth, Krantz, Jaworski, Leanza, and Feruglio.

The absence of marine Jurassic rocks in eastern North America suggests an interval of erosion. During the second half of the past century the Rocky Mountain and Pacific Coast areas were investigated by several national exploration surveys, including the U. S. Geological Survey, and by the Geological Survey of California from 1860 to 1869. A shallow western interior sea spread southward from Canada through parts of the Rocky Mountain region into Arizona but was separated from the Pacific Coast embayments by a north and south axial land mass which extended northward through Nevada and eastern California. Discussions of these rocks have been published in the numerous reports of the U. S. Geological Survey, in state reports, and in the geological journals and bulletins. The Jurassic marine formations of the Pacific Coast basins were described in the reports of the Transcontinental Railway Surveys, of the Geological Survey of California, the Geological Survey of Canada, the California Academy of Sciences, the present State of California Division of Mines, and by numerous independent authors connected with the universities.

Cretaceous: The many papers, monographs, and maps concerning Cretaceous rocks of western Europe published during the first half of the nineteenth century made known the principal stratigraphic units and their classification. Among the more important contributors were Leymerie, d'Orbigny, Buvignier, and d'Archiac in France; F. von Roemer, Hans Geinitz, and Emmanuel Reuss in Germany and Austria.

During the past one hundred years investigations of the Cretaceous of Europe have involved detailed studies of the lithology and faunas of particular areas, the correlation of different stratigraphic units from one area to another and the establishment of faunal zones. Barrois in 1876 attempted to correlate the

Upper Cretaceous succession of England with that of northern France. Coquand carried on detailed investigations in southern France, where the rocks show marked facies variations, and tried to correlate the divisions with those established by Hebert in the north of France. The regression of the seas late in Jurassic time left extensive areas of Europe just barely above sea level and upon this surface in southern England was deposited the Wealden formation, with its rich vertebrate fauna.

The east-west Vindelican land mass which divided Europe into two east-west basins became flooded as Cretaceous time progressed, producing a succession of overlapping beds from southern to northern France so that by Middle Cretaceous time the sea transgressed widely over Europe. Farther east in the Himalaya region of Tethys Basin an extensive series of Cretaceous sediments contained an eastern facies of the Alpine faunas, as described by Victor Uhlig and Stoliczka.

Extensive outcrops of folded and faulted Cretaceous rocks, which lie in the great downfold extending westward through northern Venezuela and thence southward in the Andean trough from Colombia into southern Argentina and Chili, have been described by the geologists connected with the national surveys of those countries and by independent scientific investigators. The faunas of the successive stages show close relationships to those of Europe. The Cretaceous faunas of central Argentina have many affinities with those of the Uitenhage formation of South Africa. Among the more important contributors to these problems are Behrendsen, Burckhardt, Groeber, Windhausen, Gerth, Ortmann, Krantz, Stanton, Leanza, and Feruglio.

The Federal and state survey reports in north America during the second half of the past century present a fairly clear picture of the areal distribution of Cretaceous rocks in the Atlantic and Gulf Coastal Plains, the Rocky Mountain region, and the Pacific Coast. During the past fifty years detailed studies of particular areas have been undertaken by the geologic staffs of oil companies and a part of this information has been published by the American Association of Petroleum Geologists, the Geological Society of America, and other similar organizations.

Late in the Jurassic and axial uplift west of the Rocky Mountains was accompanied by a broad north and south downwarp extending from northern Canada to Mexico and within it were deposited a nearly complete succession of marine Middle and Upper Cretaceous sediments. These formations and their faunas have been described in the numerous reports and geologic folios of the U. S. Geological Survey and other state and private organizations. For many years there was uncertainty concerning the boundary between the uppermost Cretaceous and basal Tertiary, a time of withdrawal of marine seas from the trough and of the sharp tectonic disturbances which accompanied the Laramide Revolution. For some time there were controversies whether the top of the Cretaceous should be placed at the upper level of the Laramie or Fort Union beds. The land plants in the Laramie at first were thought to be related to the Tertiary but the dinosaurs were distinctly Cretaceous and are not known in the Fort Union beds. Investigations by Earling Dorf in 1940 revealed that the floras of the two formations were distinct, and the plane of demarcation now is placed at the top of the Laramie.

The studies made by the Geological Survey of California from 1860 to 1869 showed the existence in the Coast Ranges of thousands of feet of folded marine Cretaceous and late Jurassic sediments, the fossils of which were described by W. M. Gabb and others. Later studies by T. W. Stanton in 1895 showed that these deposits extend northward to Shasta County. During the past fifty years many important papers have been published by F. M. Anderson, with classifications of the sediments and descriptions of faunas. The Knoxville series, or lower part of the sequence of beds, was assigned by him to the Upper Jurassic and the remainder was considered to represent most of Cretaceous time.

Tertiary: By 1850 the broad outlines of classification of the Tertiary of Europe had been established but there were uncertainties concerning the base and top in the Alpine region owing to the complicated structures and the lack of diagnostic fossils. The memoirs of Galeotti in 1837 were followed by those of Dumont in 1849–1852, in which the Belgian Tertiary was subdivided into eleven stages, with the recognition of a series of paleontological zones. Lyell placed the lower eight stages in the Eocene, the Bolderien in the Miocene, and the Diestien and Scaldisien in the Pliocene.

Prestwich in 1857, after a study of the Tertiary deposits in the Hampshire and London basins, compared the different formations with those determined in the Paris and Belgian areas and correlated the Thanet sands with the Heersien, the London Clay with the Lower Yprésien of Belgium. In 1846 Phillipi, after a study of the Tertiary fossils of Italy, pointed out that a number of living species were present in the Pliocene but this was considered impossible by d'Orbigny and Agassiz, who regarded the fauna of each stage as an independent unit of special creation.

D'Orbigny in 1852 divided the Tertiary deposits of France into four stages, naming them in downward succession as Subapennine, Falunien, Parisien, and Suessonien, the last two being regarded by Lyell as Eocene. This classification has been greatly modified and enlarged during the past one hundred years.

The Tertiary deposits and their faunas in the Vienna Basin have been the subject of special study for over a century. After the publications by Bronn in 1837, d'Orbigny in 1846, and Reuss in 1848 these deposits were intensively investigated by Suess, whose important memoir in 1868 presented a detailed description of the Tertiary deposits between the Alps and the Manhart Range. He made known the sequence of beds and their lithologic characters and showed that the Eocene Nummulitic limestone is succeeded in turn by marls, clays, and the Meletta shales, which form an important stratigraphic horizon from the Carpathians westward through the Alps and into southwestern Germany. Above these in the Vienna Basin are freshwater beds of Eggenburg and Molt, which are succeeded by the brackish-water *Cyrena* beds and marine clays and limestones, which he referred to as the Mediterranean stage. These again are covered by brackish-water sands and clays, which are widely spread in the south of Europe and designated as the Sarmatian stage. These in turn are followed by the *Congeria* clays and conglomerates of freshwater origin, which he regarded as having been deposited by streams flowing northward from the Alps. He called these last beds the Pontic stage and referred them to the Pliocene. This important investigation made possible the establishment of a parallel between the Tertiary rocks of the entire Balkan area and the region eastward, in the vicinity of the Black and Caspian seas.

The Tertiary rocks of Germany occur in the North German Plain, the Rhineland Basin, and the Schwabian-Bavarian Plateau. The areas of outcrop in northern Germany are relatively small and disconnected, and sections with a complete succession of formations are almost nonexistent, rending it difficult to make direct correlations with the well-established stages elsewhere in western Europe. The Tertiary beds in the Maintz Basin were studied by Sandberger (1858–1863) and divided into nine paleontological zones, which were correlated with the stages of Dumont in Belgium.

The investigations of Heinrich Beyrich during the middle and second half of the past century shed much light on the North German Tertiary deposits and his detailed studies of the invertebrate faunas led to important refinements in the classification and correlation of the strata. In 1847 he correlated the Septarian clays of north Germany with the Rupelian stage of Belgium because of the identity of fossils. In 1853 in his mongraph on the *North German Tertiary Deposits* he showed that the fossil species in beds between Magdeburg and Egeln, which he considered Miocene, contained many forms characteristic of older horizons and correlated these strata with the Lower Tongrian of Belgium and the Septarian clay with the Rupelian. In 1854 he proposed that these stages, both in Germany and Belgium, should be regarded as an independent series, which he named Oligocene, subdividing this into lower, middle, and upper members. This new unit in the geologic time scale was generally accepted by European geologists and later in the nineteenth and early in the present century was widely used in North America.

The Tertiary deposits in the Schwabian-Bavarian Plateau occupy an intermediate position between the Swiss and Austrian areas. They were investigated in great detail by Bernhardt Studer, who in 1855 published his *Geologie der Schweiz.* He recognized a Jura and sub-Alpine group of deposits, the former consisting of a lower marine division with fossils similar to those in the Mainz Basin and an upper series of freshwater limestones and marls which he considered Upper Miocene. The sub-Alpine deposits, consisting of freshwater red marls, molasse, sandstone, and beds containing brown coal, extend southwest into the Rhone Valley. The marine fossils obtained from these beds were studied by K. Mayer (1858) who divided the Tertiary deposits into eleven paleontological zones. These stages in ascending order were named Garumnien, Suessonien, Londonien, Parisien, Bartonien, Ligurien, Tongrien, Aquitanien, Helvetien, Tortonien, and Astien. The first five were assigned to the Eocene, the Helvetien and Tortonien to the Miocene, and the Astien to the Pliocene. In Bavaria the sub-Alpine deposits which lie immediately north of the limestone mountains consist of flysch deposits of Eocene and Lower Oligocene age. These were described in 1861 by Gümbel with a full analysis of the fossils. The peculiar lithologic and paleontologic development of the Tertiary deposits in different geological provinces present great difficulties in making exact correlations from one area to another, and many papers have appeared in the past fifty years which attempt to solve such problems. The fundamental classifications established in Europe have been used as a standard for investigation of the Tertiary in other parts of the globe, but not always with success.

The marine Tertiary deposits of North America are confined to the Atlantic and Gulf Coastal Plains and the Coast Ranges of the Pacific slope. The deposits on the eastern border are relatively thin and, although slightly warped, possess a low seaward dip. In places the thickness is much greater in the Gulf area, where the sediments accumulated in part as delta deposits. On the Pacific Coast thicknesses of as much as 30,000 feet are recorded of both coarse and fine-grained sediments which were deposited in downwarped and faulted basins. Prior to 1850 the general character of the Tertiary in eastern North America was made known through the investigations of T. A. Conrad and others connected with newly organized state geological surveys. Thick deposits of sandstone, conglomerate, and shale of fluviatile, lacustrine, and alluvial origin which range in age from Paleocene to Pliocene are widely distributed throughout the western interior of the United States and Canada. In the Great Basin area there are several thousand feet of igneous rocks, including tuff, ash, lavas, and intrusive dikes. There has been much uncertainty concerning the age of the continental deposits but an increasing knowledge of the evolutionary development of the fossil vertebrates, together with evidence from fossil plants, is making possible an acceptable scheme of correlation.

The investigations made by W. B. Clark on the marine stratigraphy and paleontology of the Tertiary of Maryland and the contributions of E. W. Berry on fossil plants, together with papers by G. D. Harris, W. P. Woodring, Julia Gardner, C. W. Cooke, W. H. Dall, K. V. W. Palmer, and many others have aided in establishing the stratigraphic relationships of the many differing deposits in the Atlantic and Gulf coastal plains. The importance of these formations in connection with the occurrence of oil and gas has led to the publication of many stratigraphical and faunal papers by geologists on the staffs of the oil companies. The value of foraminifera for determining the age of strata otherwise deficient in diagnostic fossils has made possible a more refined classification of the Tertiary of this area and the correlation of strata which show marked lithologic changes in relatively short distances.

The Tertiary deposits in California, Oregon, Washington, and British Columbia were made known during the middle of the past century through the investigations of the Transcontinental Railway Surveys, the Wilkes Exploring Expedition, and the Geological Survey of California. In California fossiliferous rocks in the vicinity of Tejon Pass were pronounced of Eocene age and ultimately became known as the Tejon formation. Farther north in the Coast Ranges other fossiliferous strata thought to be of the same age were also referred to under that name. In 1896 investigations by T. W. Stanton, of the U. S. Geological Survey, and J. C. Merriam, of the University of California, showed that the Martinez beds in central California which at first had been considered Upper Cretaceous should be regarded as Lower Eocene. From this time until 1917 the Eocene of California was classified as Martinez and Tejon. During the early part of the present century the Eocene rocks and faunas were investigated by students and faculty of Stanford University and the University of California and the scientific results were published in the *Proceedings* of the California Academy of Sciences and the *Bulletins* of the Department of Geology at the University of California. Many investigations were carried on by the U. S. Geological Survey, with the publication of geological maps and reports. Studies made by R. E. Dickerson, B. L. Clark, Ralph Arnold, C. A. Waring, A. C. Lawson, J. C. Branner, F. M. Anderson, M. A. Hanna, G. D. Hanna, R.

Chaney, and others led to the subdivision of the Eocene into seven stages, designated by Clark and Vokes in 1936 as Martinez, Meganos, Capay, Domengine, Transition, Tejon, and Gaviota. These units have been set up largely on evidence afforded by molluscan, echinoid, and coral faunas. During the past thirty years parallel classifications have been based on foraminifera and an important standard grouping of faunal zones for the Eocene has been proposed by Boris Laiming. A similar scheme for classifying the Miocene on the basis of foraminiferal zones was proposed by R. M. Kleinpell and at the present time is widely used on the Pacific Coast. The Tertiary formations of Oregon and Washington correspond with some modification to the classifications set up in California, except that the Oligocene is much better developed. The extensive literature resulting from investigations made by geologists of the oil companies, the universities, the State of California, and the U. S. Geological Survey is laying the foundation for a clear understanding of the geological history of the Tertiary period on the Pacific Coast. Much of this information has been brought together and interpreted in the important volume on the geology of California by R. D. Reed (1933).

The stratigraphic succession of Tertiary rocks and their faunas in Japan is being made known through many publications in that country. The important paleontological contribution by W. S. Slodkewitsch on the Tertiary of the Kamchatka Peninsula in northeastern Siberia shows clearly the close relations of these faunas to the Tertiary of Alaska and Oregon and Washington.

In the East Indies for over fifty years, beginning about 1880, K. Martin published extensively on the faunas of the Tertiary, determining the ages of the beds largely by means of the percentage of living species present in the faunas. Because of the long distance from the standard European section, correlations with it were difficult. Later in 1931 Leupold and Van der Vlerck elaborated a letter system of classification, from "a" to "h," for the Tertiary of this region, basing it mostly upon the larger foraminifera, and not relating it in detail to the European classification.

The continental Tertiary deposits of the Western interior region were studied by the geologists of the Federal exploration surveys and later by the U. S. Geological Survey, the American Museum of Natural History, and the geologists and paleontologists connected with universities and state and private museums. The rich collections of fossil vertebrates were at first made known by Cope and Leidy, and later during the present century by Osborne, Matthew, Sinclair, Scott, Lull, Lucas, Loomis, Merriam, Stock, Stirton, and many others. Correlation of deposits in widely scattered areas have been based on studies of the evolutionary development of fossil mammals. The contributions to the fossil floras of the Tertiary by A. C. Seward, D. H. Scott, F. H. Knowlton, E. W. Berry, R. W. Chaney, E. Dorf, and many others have been influential in the correlation and classification of the nonmarine Tertiary deposits of North America.

Quaternary: The unconsolidated surface deposits between the uppermost Tertiary strata and sediments now in course of deposition in England and the plains of Germany were described by Buckland in 1823 as the Diluvium and were thought to have been carried over the land surface by the waters of the Biblical deluge. In 1839 the name Pleistocene was proposed by Lyell for these deposits. Agassiz (1840), who in his youth had studied the action of living glaciers in the Alps, considered that at an earlier time these glaciers had extended out on to the plains, where they formed great ice sheets, and that such conditions had occurred over large areas of the continent. The Diluvium of northern Europe is largely of glacial origin and the Quaternary was thought to have opened as continental glaciation began. In later years Quaternary time was divided into Pleistocene and Recent, the latter representing the interval between the last withdrawal of the ice and the present. Usually this interval has been considered to be about 25,000 years, but carbon[14] studies indicate that it may be only slightly more than 10,000 years. In certain parts of the world, as in Greenland and Antarctica, continental ice still persists, whereas in the tropical areas, except at high altitudes, it never existed even during the Pleistocene.

Long continued investigations in North America by Alden, Antevs, Chamberlain, De Geer, Leverett, Bretz, Matthes, Flint, and others have led to the recognition of four glacial epochs, during which the ice sheets advanced southward from Labrador and north central Canada halfway down into the United States, and three interglacial epochs, when the ice completely retreated leaving the surface which it had occupied covered with debris carried in and on the ice from northern regions. Each successive glacial deposit rests unconformably upon the much-weathered and eroded surface of the one beneath and it was largely from the interpretation of such data that distinct glacial intervals were recognized. Such studies have made possible an interpretation of the geologic history of the Quaternary.

Regions in lower latitudes which were only indirectly affected by glaciation have a history characterized by erosion, deformation, and accumulation of sediments similar to that of the Pliocene and older epochs, as in the Coast Ranges of California where thick deposits of Pleistocene and Recent sands, clays, and gravels of both marine and continental origin accumulated. In many places these strata have been folded and faulted, with evidence of local diastrophism during the Pleistocene.

Submarine Investigations: During the past twenty-five years intensive geological studies of the floor of the ocean have been initiated by F. P. Shepard, Maurice Ewing, and Ph. H. Kuenen, and their students. This work has demonstrated that many of the classic concepts of the ocean floor and of geologic processes in the ocean are based on inadequate data and need to be revised. Scholars are now making highly significant discoveries and have demonstrated the existence of great submarine valleys, mountain chains, and escarpments, and have found fossiliferous materials of Cretaceous and Tertiary ages in areas far distant from present land areas. Many important developments affecting historical geology may be expected from this field in the near future.

SELECTED BIBLIOGRAPHY

Agassiz, Louis

1833–1844. Recherches sur les poissons fossiles. 6 vols. Neuchâtel.

1840. Études sur les graciers. 346 pp., 32 pls. Neuchâtel.

Alberti, F. A. von

1834. Beitrag zu einer Monographie des Bunten Sandsteins, Muschelkalks und Keupers, und die Verbindung dieser Gebilde zu einer Formation. xx + 366 pp., 2 pls. Stüttgart and Tübingen.

Alexander, C. I.

1933. Shell structure of the Ostracode genus *Cytheropteron*, and fossil species from the Cretaceous of Texas. Journ. Paleont., 7:181–214, pls. 25–27.

Anderson, F. M.

1902. Cretaceous deposits of the Pacific Coast. Proc. Calif. Acad. Sci., ser. 3, 2:1–54.

Anderson, F. M., and G. Dallas Hanna

1925. Fauna and stratigraphic relations of the Tejon Eocene at the type locality in Kern County, California. Occ. Pap. Calif. Acad. Sci., No. 9. 249 pp., 16 pls.

Andrussov, N.

1897–1912. Die sudrüssischen Neogen Ablagerungen. Verh. Russ. K. Mineral. Ges., 34:195–242; 36:101–170; 39:337–495.

Angelin, N. P.

1854. Palaeontologia Scandinavica. Fasc. 2, pp. 21–92, pls. 25–41. Leipzig.

Antevs, E.

1929. Maps of the Pleistocene glaciations. Bull. Geol. Soc. Amer., 40:631–720.

Archangelski, A. D.

1905. Dépôts paléocenes de Saratov et leur fauna. Mater. Geol. Russia., 22:1–207.

Archiac, E. d'

1834–1859. Histoire des progrès de la géologie. 8 vols.

Arnold, Ralph

1906. Tertiary and Quaternary pectens of California. U. S. Geol. Surv. Prof. Pap., 47:3–146, pls. 1–53.

Barrande, Joachim

1852–1899. Système silurien du centre de la Bohême. 7 vols. Prague and Paris.

Barrell, J.

1912. Criteria for the recognition of ancient delta deposits. Bull. Geol. Soc. Amer., 23:377–446, text figs.

Barrois, C.

1876. Recherches sur le terrain crétace supérieur de l'Angleterre et de l'Irlande. Mem. Soc. Geol. du Nord. Lille, 1(pt. 1):1–232, 1 pl., 2 maps, text illus.

Bassler, R. S., and B. Kellett

1934. Bibliographic index of Paleozoic Ostracoda. Geol. Soc. Amer. Spec. Pap., 1:1–500.

Beecher, C. E.

1891–1892. Development of the Brachiopoda. Amer. Journ. Sci., ser. 3, 41:343–357; 44:133–155.

1897. Outline of a natural classification of the Trilobites. Amer. Journ. Sci., ser. 4, 3:89–106, 181–207.

Bernard, F.

1895–1897. Note sur le développement et la morphologie de la coquille chez les Lamellibranches. Bull. Soc. Géol. France, ser. 3, 23:104–154; 24:54–82, 412–449; 25:559–566.

Bernard, H. M.

1895. The zoological position of Trilobites. Sci. Progr., 4:33.

1895. Supplementary notes on the systematic position of the Trilobites. Quart. Journ. Geo. Soc., 50:352.

BERRY, E. W.

1920. Paleobotany, a sketch of the origin and evolution of floras. Smithson. Inst. Ann. Rept. (1918), pp. 289–407.

BEYRICH, E.

1853–1856. Die Conchylien des norddeutschen Tertiärgebirges. Zeitschr. Deutsch. Geol. Ges., Vols. 5, 6, 8.

BILLINGS, E.

1861. New species of Lower Silurian fossils, Pt. I. Geol. Surv. Canada, p. 5.

1870. Notes on some specimens of Lower Silurian Trilobites, Quart. Journ. Geol. Soc. London, 26:479–486.

BITTNER, A.

1895. Revision der Lamellibranchiaten von St. Cassian: Arh. K. K. Geol. Reichsanst. Vol. 18. 235 pp. 24 pls.

BOSE, E.

1917. The Permo-Carboniferous ammonoids of the Glass Mountains, west Texas, and their stratigraphical significance. Univ. Texas Bull., 1762:1–241.

BRADY, B. H.

1884. Report on the Foraminefera dredged by H.M.S. "Challenger," during the years 1873 to 1876. "Challenger" Rept., Vol. 9. 814 pp., 115 pls.

BRANCO, W.

1880–1881. Beiträge zur Entwicklungsgeschichte der fossilen Cephalopoden Palaeontographica, 26(1880):19–50, pls. 4–13; 27(1880–1881):12–81, pls. 4–11.

BROCCHI, GIOVANNI

1814. Conchiologia fossile subapennine con osservazioni geologiche sugli Appennini, e sul suolo adiacente. 2 vols. Milan.

BRONN, H. G.

1834–1838. Lethaea geognostica. 2 vols. Stuttgart.

1848–1849. Index palaeontologicus . . . 2 vols. Stuttgart.

BROOKS, T. B.

1876. Classified list of rocks observed in the Huronian Series, south of Lake Superior. Amer. Journ. Sci., ser. 3, 12:194–204.

BRUSINA, SPIRIDON

1884. Die Fauna der Congerienschichten von Agram in Kroatien. Beitr. Palaeont. Oesterr.-Ung., 3:125–188.

BUCH, LEOPOLD VON

1834. Ueber Terebrateln, mit einem Versuch sie zu Classificiren und zu beschreiben. Abh. K. Akad. Wiss. Berlin (1833), pp. 43–60.

1837. Ueber den Jura in Deutschland. Abh. K. Akad. Wiss. Berlin (1837), pp. 49–136.

1845. Ueber Cystideen eingeleitet durch die Entwicklung der Eigenthumlichkeiten von *Caryocrinus ornatus* Say. Abh. K. Akad. Wiss. Berlin (1844), pp. 89–116, 2 pls.

BUCKLAND, WILLIAM

1823. Reliquiae Diluviane . . . vii + 303 pp., 27 pls. London.

BUCKMANN, S. S.

1909–1930. Yorkshire Type Ammonites. Vols. 1–7. London.

BURCKHARDT, CARLOS

1903. Beiträge zur Kenntnis der Jura- und Kreideformation der Cordilleren. Palaeontographica, 50:1–144, pls. 1–16.

BURMEISTER, H.

1843. Die organisation der Trilobiten. Eng. rev. ed., Roy. Soc. London (1846). vii + 136 pp., 6 pls.

CARPENTER, H.

1884–1888. Report on the Crinoidea. "Challenger" Rept. Vols. 11 and 26.

CHANEY, RALPH, and ETHEL I. SANBORN

1933. The Goshen flora of West Central Oregon. Carnegie Inst. Wash., Publ. No. 439, pp. 1–103.

CLARK, B. L., and H. E. VOKES

1936. Summary of marine Eocene sequence of western North America. Bull. Geol. Soc. Am., 47:851–878.

CLARK, W. B.

1901. The Eocene deposits of Maryland. Pp. 21–92. Maryland Geol. Surv.

CLARK, W. B., and M. W. TWITCHELL

1915. Mesozoic and Cenozoic Echinodermata of the United States. U. S. Geol. Surv. Monogr. 54, pp. 1–341, 108 pls.

CLARKE, J. M.

1893. The Protoconch of *Orthoceras*. Amer. Geol., 12:112–115.

1897. The Lower Silurian Cephalopoda of Minnesota. Minn. Geol. Surv., Final Rept. 3(2), pp. 761–812.

CLARKE, J. M., and R. RUEDEMANN

1912. The Eurypterida of New York. N. Y. State Mus. Mem. 14. 2 vols.

COLEMAN, A. P.

1908. The Lower Huronian ice-age. Journ. Geol., 16:148–158, figs.

1915. The Proterozoic of the Canadian Shield. *In* Problems of American Geology, pp. 81–161. Yale Univ. Press.

COLLINS, W. H.

1922. An outline of the physiographic history of north-eastern Ontario. Journ. Geol., 30:199–210, figs.

CONRAD, T. A.

1832–1833. Fossil shells of the Tertiary formations of North America. Pp. 1–56. Philadelphia.

1837. Description of new marine shells from Upper California. Journ. Phila. Acad. Nat. Sci., 7(pt. 2):227–268.

1842. Observations on the Silurian and Devonian systems of the United States. Journ. Phila. Acad. Nat. Sci., 8:228, 280.

CONYBEARE, W. D., and WILLIAM PHILLIPS

1822. Outline of the Geology of England and Wales, with an Introductory Compendium of the General Principles of that Science and Comparative Views of the Structure of Foreign Countries. lxi + 470 pp., 2 pls., 1 map, text illus. London.

COSSMANN, M.

1895–1925. Essais de paléoconchologie comparée. Vols. 1–13. Paris.

Cummings, E. R.

1903. The morphogenesis of *Platystrophia;* a study of the evolution of a Paleozoic brachiopod. Amer. Journ. Sci., 15:1–48, 121–136.

Cushman, J. A.

1940. Foraminifera. Their Classification and Economic Use. 3d ed. 535 pp., 48 pls. Cambridge, Mass.

Cuvier, Georges

1811–1812. Recherches sur les Ossemens fossiles. . . . 4 vols. Paris.

Cuvier, Georges, and Alexandre Brongniart

1808. Essai sur la géographie mineralogique des environs de Paris. Pp. 1–278, 1 pl. Paris.

Dall, W. H.

1890–1903. Contributions to the Tertiary fauna of Florida. Trans. Wagner Free Inst. Sci. Phila., Vol. 3, pts. 1–6, pp. 1–1634, pls. 1–60.

Dalman, J. W.

1827. Om Palaeaderna, eller de så kallade Trilobiterna. Handl. K. Svensk. Vet.-Acad. (1826), pp. 113–152; 226–294, pls. 1–6.

Dana, J. D.

1862. Manual of Geology. 798 pp. Philadelphia.

1872. Green Mountain geology: on the Quartzite. Amer. Journ. Sci., ser. 3, 3:179–186, 250–256.

Darton, N. H.

1928. Red beds and associated formations in New Mexico. U. S. Geol. Surv., Bull. 794, pp. 1–356.

Darwin, Charles

1859. The Origin of Species by Means of Natural Selection. ix + 502 pp., 1 pl. London.

David, T. W., and C. A. Sussmilch

1931. Upper Paleozoic glaciation of Australia. Bull. Geol. Soc. Amer., 42:481–522.

Davidson, Thomas

1851–1886. British fossil Brachipoda. 6 vols. London: Palaeont. Soc.

Davies, A. M.

1934–1935. Tertiary Faunas. 2 vols. London: Thomas Murby and Co.

Davis, W. M.

1886. Relation of the coal of Montana to the older rocks. 10th U. S. Census, 15:697–712.

Depéret, C., and F. Roman

1902. Monographie des Pectinides néogènes de l'Europe et des régions voisines. 1re partie. Genre *Pecten.* Mém. Soc. Géol. France, Paleont., 10(26):1–73, figs., pls. 1–8.

Deshayes, G. P.

1824–1837. Description des coquilles fossiles des environs de Paris. 2 vols. Paris.

Dickerson, R. E.

1914. Fauna of the Martinez Eocene of California, Univ. Calif. Publ. Bull. Dept. Geol., 8:61–180, pls. 6–18.

Diener, C.

1897. Himalayan fossils, Palaeont. Indica, ser. 15, 1(pt. 3):1–105, pls. 1–13.

Dorf, E.
1940. Relationship between floras of the type Lance and Fort Union formations, Bull. Geol. Soc. Amer., 51:213–235.

Douville, H.
1906. Sur la structure du test dans les fusulines. Compt. Rend. Acad. Sci. Paris, 143:258–261.
1907. Evolution et enchaînement des Foraminifères. Bull. Géol. Soc. France, ser. 4, 6:588–602, 1 pl.
1912. Classification des Lamellibranches. Bull. Geol. Soc. France, ser. 4, 12:419–467.

Dujardin, F.
1835. Observations sur les Rhizopodes et les Infusoires. Compt. Rend. Acad. Sci. Paris, pp. 338–340.

Dumont, A.
1849. Rapport sur la carte géologique du Royaume. Bull. Acad. Roy. Belgique, ser. 1, vol. 16, pt. 2, pp. 351–373.

Dumortier, Eugene
1864–1874. Études paléontologiques sur les jurassiques du bassin du Rhone. 4 vols. Paris.

Dunbar, C. O., and G. E. Condra
1932. Brachiopods of the Pennsylvanian system of Nebraska. Neb. Geol. Surv., ser. 2, Bull. 5, pp. 1–377.

Eastman, C. R., ed.
1913. Textbook of Paleontology, Adapted from the German of Karl A. von Zittel. Vol 1. 839 pp., 1594 figs. New York: Macmillan and Co.

Emmons, E.
1842. Geology of New York. Pt. 2, Comprising the Survey of the Second Geological District. 437 pp. Albany.

Emmrich, H.
1845. Ueber die Trilobiten. Neues Jahrb. Mineral., pp. 18–62, 1 pl.

Éstallon, A.
1859–1861. Études paléontologiques sur les terrains jurassiques du Haut-Jura. 2 vols., App. Paris.

Feruglio, Egidio
1950. Descripción geológica de la Patagonia, Republica Argentinica, Dirección General de Yacimientos Petroliferos Fiscales. 3 vols., 1107 pp.

Fitton, W. H.
1836. Observations on some of the strata between the Chalk and Oxford Oolite in the south-east of England. Trans. Geol. Soc. London, ser. 2, 4:103–400.

Fleming, J.
1828. History of British Animals. xxiii + 565 pp. London.

Foerste, A. F.
1921. Notes on Arctic Ordovician and Silurian cephalopods. Journ. Denison Univ., Bull. Sci. Labor., 19:247–306, 9 pls.

Fromentel, L. E. G. de
1859. Introduction à l'étude des éponges fossiles. Pt. 1 (all published) Mem. Soc. Linn. Normandie, Caen, 11(no. 2):1–50, 4 pls.

Fucini, A.

1897. La Fauna del Lias medio del Monte Calvi. Palaeontol. Italica, 2:203–250, pls. 24–25.

Gabb, W. M.

1864–1869. Description of the Cretaceous and Tertiary fossils of California, Paleontology of California, Geo. Surv. Calif. 2 vols.

Galloway, J. J.

1933. Manual of Foraminifera. 483 pp. Bloomington, Ind.: The Principia Press.

Gardner, Julia

1935. The Midway group of Texas. Texas Univ. Bull., 3301:1–403, pls. 1–28.

Geinitz, H. B.

1842. Charakteristic der Schichten und Petrefacten des sächsischen Kreidegebirges. 116 pp. Dresden.

1856. Geognostische Darstellung der Steinkohlenformation in Sachsen, Die Steinkohlen des Königreiches Sachsen . . . Abt. 1.

Gemmellaro, G. G.

1868–1876. Studi paleontologici sulla Fauna del Calcario a Terebratula janitor del nord di Sicilia. Nos. 1–3. Palermo.

1887–1890. La Fauna dei Calcari con Fusulina della Valle del Fuime Sosio nella Provincia de Palermo. Giorn. Sci. Nat. e Econ., 19:1–106, 10 pls.; Appendice, 20:9–138, 13 pls.

1904. I Cefalopodi del Trias superiore della regione occidentale della Sicilia. Giorn. Soc. Sci. Nat. Palermo, 24:1–321, 30 pls.

Gerth, Hans

1926. Beiträge zur Palaentologie und Stratigraphie des Lias, Doggers, Tithons, und der Unterkreide in den Kordilleren im Süden der Provinz Mendoza (Argentinien):III. Die Fauna des Neokom in der argentinischen Kordillere, geologischen Rundschau. 17a:463–494, pls. 18–19.

Girty, G. H.

1908. The Guadalupian Fauna. U. S. Geol. Surv., Prof. Pap. 58, 651 pp., 31 pls.

1910. New species of fossils from the Thaynes limestone of Utah. Ann. New York Acad. Sci., 20:239–242.

Glaessner, M. F.

1945. Principles of Micropaleontology. 296 pp. Australia: Melbourne Univ. Press.

Goldfuss, G. A.

1843. Systematische Uebersicht des Trilobiten und Beschreibung einiger neuen Arten. Neues Jahrb. Mineralog., p. 537 *et seq.*, 3 pls.

Goldfuss, G. A., and G. Munster

1826–1840. Petrefacta Germaniae. Vols. 1–2.

Grabau, A. W.

1904. Phylogeny of Fusus and its allies. Smithson. Misc. Coll., 44(1417):1–192.

Grant, Robert

1825–1827. Observations and experiments on the structure and functions of the sponges. Edinburgh Philos. Journ., Vols. 8, 9; New Edinburgh Philos. Journ., Vol. 2.

Grant, U. S., IV, and H. R. Gale

1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. Mem. San Diego Soc. Nat. Hist., No. 1, pp. 1–1036, pls. 1–32.

GRANT, U. S., IV, and L. G. HERTLEIN

1938. The West American Cenozoic Echinoidea. Publ. Univ. Calif. Los Angeles Math. and Phys. Sci., 2:1–225, pls. 1–30.

GÜEMBEL, C. W.

1858–1861. Geognostiche Beschreibung des bayerischen Alpengebirges. Gotha, pp. 1–429.

1861. Geognostische Beschreibung des bayerischen Aplengebirges und seines Vorlandes. Gotha, pp. 1–950.

HALL, JAMES

1843. Geology of New York. Pt. IV, comprising the survey of fourth geological district, pp. 1–683. Albany.

HALL, JAMES, and J. M. CLARKE

1898. A memoir of the Paleozoic reticulate sponges constituting the family Dictyospongidae. State Geol. Surv., New York, Ann. Rept. (1898), pp. 754–984, pls. 1–47, text figs.

HANDLIRSCH, A.

1906. Revision of American Paleozoic insects. Proc. U. S. Nat. Mus., 29:661–820.

HARRIS, G. D.

1896. The Midway Stage. Bull. Amer. Paleont., 1(no. 4):1–125.

1897–1899. The Lignitic Stage. Bull. Amer. Paleont., 2(no. 9):1–74; 3(no. 11):1–103.

HAUER, F.

1858–1859. Beiträge zur Palaeontographie von Oesterreich, bd. 1: (hefte 1–2), pp. 1–64, pls. 1–14.

HEINRICH, M.

1914. Studien in den Riffkalken des rheinischen Mitteldevons. Zbl. f. Min. usw., pp. 732–736 (also in Journ. Geol., 24:57–60).

HOERNES, R.

1903. Zur Ontogenie und Phylogenie der Cephalopoden. Jahrb. K. K. geol. Reichsanst., 53:1–32.

HOERNES, R., and M. AUINGER

1879–1891. Die Gasteropoden der Meeres-ablagerungen der ersten und zweiten miocänen Mediterran-stufe in der Oesterreichisch-Ungarischen Monarchie. 382 pp., 50 pls. Vienna.

HUDLESTON, W. H.

1887–1896. A Monograph of the British Jurassic Gastropoda. Palaeont. Soc. London. 514 pp., 44 pls.

HUNT, T. STERRY

1873. The geognostical history of the Metals. Trans. Amer. Inst. Min. Eng., 1:331–345; 2:58–59.

HYATT, ALPHEUS

1872. Fossil cephalopods of the Museum of Comparative Zoology, Embryology. Bull. Mus. Comp. Zool., 3:59–111.

1884. Genera of fossil cephalopods. Proc. Boston Soc. Nat. Hist., 22:253–338.

1889. A Genesis of the Arietidae. Mem. Harvard Mus. Comp. Zool., 16(3). xi + 238, figs.

JACKSON, R. T.

1890. Phylogeny of the Pelecypods; the Aviculidae and their allies. Mem. Boston Soc. Nat. Hist., 4:277–400.

1912. Phylogeny of the Echini. Mem. Boston Soc. Nat. Hist., 7:1–491, pls. 1–76.

JAWORSKI, E.

1915. Beiträge zur Kenntnis des Jura in Sudamerika. Pt. 2. Neues Jahrb. Mineralog. Suppl. 40, pp. 364–456.

KARPINSKY, A. P.

1874. Geologic explorations in Orenburg district. Abh. K. Mineralog. Ges. St. Petersburg, ser. 2, 9:212–310.

1889. Über die Ammoniten der Artinsk-Stufe und einige mit denselben verwandte carbonische Formen. Mem. Acad. Imp. Sci. St. Petersburg, ser. 7, 37:1–104.

KEEN, A. MYRA, and HERDIS BENTSON

1944. Check list of California marine Mollusca. Geol. Soc. Amer., Spec. Pap. 56, pp. 1–280.

KEW, W. S. W.

1920. Cretaceous and Cenozoic Echinoidea of the Pacific Coast of North America. Univ. Calif. Publ. Bull. Dept. Geol., 12:23–236, pls. 3–42.

KING, W.

1846. Remarks on certain genera belonging to the class Palliobranchiata. Ann. and Mag. Nat. Hist., 18:26–42, 83–94.

KITCHIN, F. L.

1903. The Jurassic fauna of Cutch. Palaeontol. Indica, ser. 9, 3(1):1–87, 14 pls.

1913. The invertebrate fauna and paleontological relations of the Uitenhage series. Ann. So. African Mus., 7:21–250.

KLEINPELL, R. M.

1938. Miocene Stratigraphy of California. 459 pp., 27 pls. Tulsa: Amer. Assoc. Petrol. Geol.

KOENEN, A. VON

1889–1894. Das norddeutschen Unter-Oligocän und seine Mollusken-Fauna. Abh. Geol. Specialk. Preuss. u. Thuring. Staat., 10(pts. 1–7):1–1458.

1902. Die Ammonitiden der norddeutschen Neocom. Abh. K. Preuss. Geol. Landesanst., Heft 24, pp. 1–451, pls. 1–55.

KONINCK, L. G. DE

1842–1851. Description des animaux fossiles qui se trouvent dans le terrain carbonifère de Belgique. 716 pp., 60 pls. Liege.

KOZLOWSKI, R.

1948. Les graptolithes et quelques nouveaux groupes d'animaux du Tremadoc de la Pologne. Palaeontol. Polonica, 3:1–235, pls. 1–42.

KREJCI-GRAF, K., and W. WENZ

1931. Stratigraphie und Paläontologie des Obermiozäns and Pilozäns der Muntenia (Rumänien). Zeitschr. Deutsch. Geol. Ges., 83:65–163, figs., pls. 1–2.

KUNTH, A.

1869–1870. Beiträge zur Kenntniss fossiler Korallen. Zeitschr. Deutsch. Geol. Ges., 21:647–688, pls. 18–19; 22:24–43, pl. 1.

LAIMING, BORIS

1940. Some foraminiferal correlations in the Eocene of San Joaquin Valley, California. Proc. 6th Pac. Sci. Congr., pp. 535–568.

LAMARCK, J. B. P. M. DE

1815–1822. Histoire naturelle des animaux sans vertèbres. Vols. 1–7. Paris.

LAMBERT, J., and P. THIÉRY

1909–1925. Essai de nomenclature raisonnée des echinides. 600 pp., 15 pls. Chaumont.

LAWSON, A. C.

1885. Report on the geology of the Lake of the Woods region, with special reference to the Keewatin (Huronian?) belt of the Archean rocks. Canad. Geol. Surv. Ann. Rept. 1, 151 pp., map.

1913. The Archean geology of Rainy Lake restudied. Canad. Geol. Surv., Mem. 40, pp. 1–115.

LEANZA, A. F.

1945. Ammonites del Jurassicco superior y del Cretaceo inferior de la Sierra Azul, Mendoza. Anal. Mus. la Plata, n.s., Paleont., Sec. A, 6(no. 1):1–99, pls. 1–23.

LEYMERIE, A.

1840. Mémoire sur le terrain Crétace du department de l'Aube. Mem. Soc. Géol. France, ser. 1, 4:291–364.

LINNAEUS, CARL

1758. Systema Naturae. 10th ed. 824 pp.

LOGAN, W. E.

1863. Report on the geology of Canada. Can. Geol. Surv. Rept. Prog. to 1863. 983 pp.

LOTTNER, F. H.

1859. Geognostische Skizze des westfälischen Steinkohlengebirges. Erlauternder Text sur Flötzkarte des westfälischen Steinkohlengebirges, Iserlohn.

LOVÉN, SVEN

1874. Études sur les Echinoides. Handl. K. Svensk. Vet.-Akad., 11(no. 7):1–91, pls. 1–53.

LYELL, SIR CHARLES

1830–1833. Principles of Geology. 3 vols. London: Murray.

MARTIN, K.

1879–1880. Die Tertiärschichten auf Java . . . 161 pp., 28 pls., 1 map. Leiden.

1891–1922. Die Fossilien von Java. Samml. Geol. Reichsmus. Leiden. 538 pp., 63 pls.

MATTHEWS, W. D.

1915. The Tertiary sedimentary record. *In* Problems of American Geology, pp. 377–478. New Haven: Yale Univ. Press.

MAYER, K.

1858. Versuch einer neuen Classification der Tertiär Gebilde Europás, Verh. Schweiz. Natur. Wiss. Ges. (1857), 42:164–199.

MEEK, F. B.

1876. A report on the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri country. U. S. Geol. Surv. Terr., 9:1–629, pls. 1–45.

MERRIAM, CHARLES

1941. Fossil Turritellas from the Pacific Coast Region of North America. Univ. Calif. Publ., Bull. Dept. Geol. Sci., 26:1–214, pls. 1–41.

MILLER, A. K.

1938. Devonian Ammonoids of America. Geol. Soc. Amer., Spec. Pap. 14, pp. 1–262, pls. 1–39.

MILLER, J. S.

1821. A Natural History of the Crinoidea or Lily-shaped Animals. viii + 150 pp., 1 pl. Bristol.

MILLER, HUGH

1841. The Old Red Sandstone. 275 pp., 10 pls. Edinburgh.

MILNE-EDWARDS, H., and J. HAIME

1850–1854. Monograph of the British Fossil Corals. Palaeont. Soc. 322 pps., 72 pls.

1857–1860. Histoire naturelle des corallaires. Vols. 1–3, Atlas. Paris.

MOJSISOVICS, E. VON

1873–1876. Die Cephalopoden der mediterranen Triasprovinz. Abh. K. K. Geol. Reichsanst., 6:356–835.

MORRIS, J., and J. LYCETT

1850–1854. Mollusca from the Great Oolite. Palaeont. Soc., pp. 1–147, pls. 1–15.

MOSELEY, H. N.

1877. On the structure of Millepora. . . . Roy. Soc. London, Philos. Trans. 167, Pt. I, pp. 117–135, pls. 2–3.

MUIR-WOOD, HELEN M.

1928. The British Carboniferous Producti II-*Productus* (*sensu stricto*); *semireticulatus* and *longispinus* groups. Mem. Geol. Surv. Great Britain, 3:1–217, figs., pls. 1–8.

MURCHISON, R. I.

1839. The Silurian system. 2 pts., pp. xxxii + 768 pp., 53 pls., 4 maps. London.

MURCHISON, R. I., E. DE VERNEUIL, and A. KEYSERLING

1845. The Geology of Russia in Europe and the Ural Mountains. 2 vols. London.

NEUMAYR, M.

1884. Zur Morphologie des Bivalvenschlosses. Sitzber. K. Akad. Wiss. Vienna, 88:385–418.

1887. Die natürlichen Verwandtschaftsverhältnisse der schalentragenden Foraminiferen. Sitzber. K. Akad. Wiss. Vienna, 95:156–186.

NICHOLSON, M.

1886–1892. A Monograph of the British Stromatoporoids. Palaeont. Soc., 234 pp., 29 pls. London.

OGILVIE, MARIA

1896. Microscopic and systematic study of madreporian types of corals. Roy. Soc. London, Philos. Trans. (B), 187:83–346.

OKULITCH, V. J.

1943. North American Pleospongia. Geol. Soc. Amer., Spec. Pap. No. 48, pp. 1–112, pls. 1–18.

OPPEL, ALBERT

1858. Die Juraformation Englands, Frankreichs und des südwestlichen Deutschlands, nach ihren einzelnen Gliedern eingetheilt und vergleichen. 857 pp. Stuttgart.

1859. Die neueren Untersuchungen über die Zone der Avicula contorta mit besonderer Berücksichtigung der Beobachtunger M. Martin's über das Auftreten dieser Zone im Dept. Côte d'Or. Württemberg. Naturwiss. Jahresheft., Jahrg-XVI, pp. 315–325. Munich.

ORBIGNY, ALCIDE D'

1846. Foraminifères fossiles du Bassin de Vienne. 312 pp., 21 pls. Paris.

1840–1860. Paléontologie française . . . Vols. 1–6 (until 1891 by various authors). Paris.

1851. Cours élémentaire de paléontologie et de géologie, Paris. 2 vols. in 3. 382 pp., 227 figs.

OSBORN, H. F.

1929. The Titanotheres of Ancient Wyoming, Dakota and Nebraska. U. S. Geol. Surv. Monogr. 55. 2 vols.

PALMER, K. V. W.

1937. The Claibornian Schaphopoda, Gastropoda and Dibranchiate Cephalopoda of the southern United States. Bull. Amer. Paleont., 7:1–730, pls. 1–90.

PAVLOW, A. P.

1907. Enchaînements des Aucelles et Aucellines du Crétace Russe. Nouv. Mem. Soc. Imper. Nat. Moscow, Vol. 17, fasc. 1, pp. 1–93, pls. 1–6.

PEALE, A. C.

1893. The Paleozoic section in the vicinity of Three Forks, Montana. U. S. Geol. Surv. Bull. 110, pp. 1–56.

1897. Description of the Three Forks sheet. U. S. Geol. Surv., Geol. Atlas, Three Forks Fol. (no. 24). 5 pp., maps.

PELSENEER, PAUL

1906. Mollusca. *In* E. R. Lankester, A Treatise on Zoology. Vol. 5, pp. 1–355. London.

PETRUNKEVITCH, A.

1913. A monograph of the terrestrial Paleozoic Arachnida of North America. Trans. Conn. Acad. Arts and Sci., 18:1–137, pls. 1–13.

PHILIPPI, R. A.

1836–1844. Enumeratio Molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium quae in itinere suo observavit. Berolini. 2 vols. Berol. and Halis Sax.

PICTET, F. J., and G. CAMPICHE

1858–1872. Description des fossiles du terrain Crétace des environs de Sainte-Croix, Mat. Paleont. Suisse. Vols. 1–5. Geneva.

POMEL, M.

1872. Paléontologie ou description des animaux fossiles de l'Algérie, Fasc. 5 (Spongiaires), pp. 1–256, 36 pls. Oran.

POMPECKJ, J. F.

1893–1896. Beiträge zu einer Revision der Ammoniten des Schwäbischen Jura. Ver. Vaterl. Naturk., Vol. 49; Vol. 52 (178 pp., 12 pls.).

POWELL, J. W.

1875. Exploration of the Colorado River of the West and Its Tributaries. xi + 291 pp. Washington.

PRESTWICH, JOSEPH

1857. On the correlation of the Eocene Tertiaries of England, France and Belgium. Quart. Journ. Geol. Soc., 11:206–246.

QUENSTEDT, F. A.

1837. Beiträge zur Kenntniss der Trilobiten mit besonderer Rücksicht auf ihre bestimmte Gliederzahl. Wiegmann's Archiv. Naturgesch., ser. 3, 1:337–352.

1858. Der Jura, 842 pp. Tübingen.

1885–1888. Die Ammoniten des Schwäbischen Jura. 1140 pp. Stuttgart.

RANKAMA, KALERVO

1948. New evidence of the origin of pre-Cambrian carbon. Bull. Geol. Soc. Amer., 59:389–416.

RAUFF, H.

1893–1894. Palaeospongiologie. Palaeontographica, 40:1–346, pls. 1–17; 41:221–271, pls. 18–24.

RAYMOND, P. E.

1920. The appendages, anatomy and relationships of Trilobites. Mem. Conn. Acad. Arts and Sci., 7:1–169.

REED, R. D.

1933. Geology of California. Amer. Assoc. Petrol Geol. xxiv + 355 pp. Tulsa.

REESIDE, J. B., JR.

1927. The cephalopods of the Eagle sandstone and related formations of the western interior of the United States. U. S. Geol. Surv., Prof. Pap. 151, pp. 1–87.

REUSS, A. E.

1861. Entwurf einer systematischen Zusammenstellung der Foramniferen Sitzb. Akad. Wiss. Vienna, pp. 355–396.

RHUMBLER, L.

1899. Über die phylogenetisch abfallende Schalen-Ontogenie der Foraminiferen und deren Erklärung. Verh. Deutsch. Zool. Ges., pp. 162–192.

RICHTHOFEN, F. VON

1860. Geognostische Beschreibung der Umgegend von Predazzo, St. Cassian, und der Seisser Alp in Süd-Tyrol. xii + 327 pp., 4 pls., 1 map. Gotha.

ROEMER, C. F.

1844. Das Rheinische Uebergangsgebirge. Eine paläontologischgeognostische Darstellung. 96 pp., 6 pls. Hannover.

ROEMER, F. A.

1841. Die Versteinerungen des norddeutschen Kreidegebirges. iv + 145 pp., 16 pls. Hannover.

1864. Die Spongitarien des norddeutschen Kreidegebirges. Palaeontographica, 13: 1–64, pls. 1–19.

ROEMER, FERDINAND

1848. Ueber ein bisher nicht beschreibenes Exemplar von Eurypterus aus devonischen Schichten des Staates New York . . . Palaeontographica, 1:190–193.

1860. Die silurische Fauna des westlichen Tennessee. 100 pp. Breslau.

ROEMER, F. VON

1870. Geologie von Oberschlesien. Eine Erlauterung zu der . . . geologischen Karte von Oberschlesien . . . xxiv + 587, xxii [1] pp., 1 pl., text illus. Atlas, 50 pls., 14 maps and sections. Berlin.

ROGERS, H. D.

1858. The Geology of Pennsylvania, a Government Survey. 2 vols., 1631 pp. Philadelphia.

ROGERS, W. B., and H. D. ROGERS

1843. On the physical structure of the Appalachian chain . . . Assoc. Amer. Geol. Repts., pp. 70–71 (abst.), 474–531.

ROTHPLETZ, A.

1886. Geologisch-palaeontologische Monographie der Vilser Alpen, mit besonderer Brachiopoden-Systematik. Palaeontographica, 33:1–180, 17 pls.

SACCO, M. F.

1905. Les Étages et les Faunes du Bass in Tertiaire du Piémont. Bull. Géol. Soc. France, ser. 4, 5:893–916.

SALTER, J. W., and H. WOODWARD

1867–1884. A Monograph of British Trilobites, Pt. 1. Palaeont. Soc. London, pp. 1–224, pls. 1–30.

SANDBERGER, C. L. F. VON

1858–1863. Die Conchylien des Mainzer Tertiärbeckens. 458 pp., 35 pls. Wiesbaden.

SCHENCK, H. G.

1931. Cephalopods of the genus *Aturia* from western North America. Univ. Calif. Publ., Bull. Dept. Geol. Sci., 19:435–465, pls. 66–78.

1936. Nuculid bivalves of the genus *Acila*, Geol. Soc. Amer., Spec. Pap. No. 4, pp. 1–149, pls. 1–18.

SCHLOTHEIM, ERNST VON

1820–1823. Die Petrefactenkunde . . . , 3 pts., 52 pls. Gotha.

SCHUCHERT, CHARLES

1897. A synopsis of American fossil Brachiopoda. U. S. Geol. Surv. Bull. 87, pp. 1–464.

1915. Revision of the Paleozoic Stelleroidea with special reference to North American Asteroidea. U. S. Nat. Mus., Bull. 88, pp. 1–311, pls. 1–38.

1928. Middle Permian age of the late Paleozoic glaciation. [Abst.] Bull. Geol. Soc. Amer., 39:208–209.

1932 Gondwanaland bridges. Bull. Geol. Soc. Amer., 43:875–916.

SCHUCHERT, CHARLES, and G. A. COOPER

1932. Brachiopoda genera of the suborders Orthoidea and Pentameroidea. Mem. Peabody Mus. Nat. Hist., 4(pt. 1):1–270, pls. 1–29.

SCHULTZE, M. S.

1854. Ueber den Organismus der Polythalamien (Foraminiferen). + 69 pp., 7 pls. Leipzig.

SCOTT, W. B.

1913. A history of Land Mammals in the Western Hemisphere. 693 pp. New York: Macmillan and Co.

SCUDDER, S. H.

1879. Paleozoic cockroaches; a complete revision of the species of both worlds. . . . Mem. Boston Soc. Nat. Hist., 3:23–134.

1886. Systematic review of our present knowledge of fossil insects, including myriapods and arachnids. U. S. Geol. Surv. Bull. 31, pp. 1–128.

1900. Adephagous and clavicorn Coleoptera from the Tertiary deposits at Florissant, Colo. U. S. Geol. Surv., Monogr. 40, pp. 1–148.

SEDERHOLM, J. J.

1907. Om Granit och Gneis, deras Uppkomst, Uppträdande och Utbredning inom Urberget i Fenno-Scandia. (English summary) Finlands. Geolog. Undersökning, Bull. No. 23, pp. 1–110, 8 pls, 2 maps.

SEDGWICK, A.

1835. [Abst., no title]. Edinburgh, New Philos. Journ., 19:390.

1836. [First use of Cambrian]. British Assoc. Adv. Sci. Rept. 5th meeting, pp. 59–61.

SEDGWICK, A., and R. I. MURCHISON

1839. On the classification of the older rocks of Devonshire and Cornwall. [Abst.] Proc. Geol. Soc. London, 3(61):121–123.

SLODKEWITSCH, W. S.

1938. Tertiary pelecypoda from the Far East, Paleontology of U.S.S.R., Acad. Sci. USSR, vol. 10, pt. 3, fasc. 18, pp. 1–508; fasc. 19, pp. 1–275, 106 pls.

SMITH, J. P.

1897. The development of *Glyphioceras* and the phylogeny of the Glyphioceratidae. Proc. Calif. Acad. Sci., ser. 3, 1:105–128.

1903. The Carboniferous Ammonoids of America. U. S. Geol. Surv. Monogr. 42. 211 pp., 8 pls.

SMITH, J. P. (Cont.)

1914. The Middle Triassic marine invertebrate faunas of North America. U. S. Geol. Surv., Prof. Pap. No. 83. 254 pp., pls. 1–99.

1927. Upper Triassic marine invertebrate faunas of North America. U. S. Geol. Surv. Prof. Pap. 141. 262 pp., pls. 1–121.

SMITH, J. P., and A. HYATT

1905. The Triassic Cephalopod genera of America. U. S. Geol. Surv. Prof. Pap. 40. 394 pp., pls. 1–85.

SMITH, JOSHUA TOULMIN

1847–1848. Ventriculidae of the Chalk. Ann. Nat. Hist., ser. 1, 20:73–97, 176–191, pls. 7, 8; ser. 2, 1:36–48, 203–220, 279–295, 352–372, pls. 13–16.

SMITH, WILLIAM

1815. A Memoir to the Map and Delineation of the Strata of England and Wales, with Part of Scotland. xi + 51 pp., London.

SOLLAS, W. J.

1877. On *Stauronema*, a new genus of fossil hexactinellid sponges. Ann. and Mag. Nat. Hist., ser. 4, 19:1–25, pls. 1–5.

SOWERBY, JAMES

1812–1845. Mineral Conchology of Great Britain. [Cont. by James de Carle Sowerby.] 7 vols. London.

SPATH, L. F.

1934. The Ammonoidea of the Trias. Catalogue of the fossil Cephalopoda in the British Museum. Pt. 4, pp. 1–521, pls. 1–18.

STANTON, T. W.

1895. The fauna of the Knoxville Beds. U. S. Geol. Surv. Bull. 133. 132 pp., 20 pls.

1896–1899. Marine Cretaceous invertebrates. Report of the Princeton University Expedition to Patagonia. Vol. 4, pt. 1, pp. 1–43, pls. 1–10.

STEPHENSON, L. W.

1928. Major marine transgressions and regressions and structural features of the Gulf Coastal Plain. Amer. Journ. Sci., ser. 5, 16:281–298.

STEWART, R. B.

1926. Gabb's California type Gastropods. Proc. Phila. Acad. Nat. Sci., 78:287–447, pls. 20–32.

1930. Gabb's California Cretaceous and Tertiary type lamellibranchs. Phila. Acad. Nat. Sci., Spec. Publ. 3, pp. 1–314, pls. 1–17.

STOLICZKA, FERDINAND

1868–1871. Cretaceous fauna of Southern India: Pelecypoda and Gastropoda. Palaeontol. Indica, ser. 1 and 3, Vol. 1; ser. 5, Vol. 2; ser. 6, Vol. 3; ser. 8, Vol. 4.

STOYANOW, A.

1910. Ueber eine neue Brachiopodenart. Bull. Acad. Sci. of the U.S.S.R. [6], 4(11): 853–855.

1915. On some Permian brachipods of Armenia. Russ. Geolog. Kom., Trudy (Comité géologique, Mém.) n.s., No. 111, pp. 1–95.

1949. Lower Cretaceous stratigraphy in southeastern Arizona. Mem. Geol. Soc. Amer., 38:1–169, pls. 1–26.

STUDER, BERNHARDT

1851–1853. Geologie der Schweiz. 2 vols., illus. Bern.

Suess, E.

1866. Über Ammoniten. Sitzungsber. K. Akad. Wiss., Vienna. Vol. 52, Abt. 1, pp. 71–89.

1868. Über die Gliederung des Vicentinischen Tertiargebirges. Sitzungber. K. Akad. Wiss., Vienna. 58:265–279.

Thomas, Ivor.

1910. The British Carboniferous Orthotetinae. Mem. Geol. Survey Great Britain. Paleontology, 1(pt. 2):83–134.

Tryon, G. W., and H. A. Pilsbry

1879–1898. Manual of Conchology. Ser. 1, vols. 1–17. Philadelphia.

Tschernyschew, Th.

1902. Die obercarbonischen Brachiopoden des Ural und des Timan. Comité Géologique Russ., Mémo., Vol. 16, (2). vii + 749 pp., 63 pls.

Udden, J. A.

1917. Notes on the geology of Glass Mountains. Bull. Univ. Texas, 1753:3–59.

Ulrich, E. O.

1897. Lower Silurian Lamellibranchiata of Minnesota; Lower Silurian Gastropoda of Minnesota. Geol. Surv. Minn., 3(pt. 2):475–628, 813–1081.

Ulrich, E. O., and R. S. Bassler

1923. Paleozoic Ostracoda, their morphology, classification and occurrence. Maryland Geol. Surv., Silurian, pp. 271–391, 18 figs.

Ulrich, E. O., and R. Ruedemann

1931. Are graptolites Bryozoans? Bull. Geol. Soc. Amer., 42:589–604.

Van Hise, C. R., and C. K. Leith

1911. The geology of the Lake Superior Region. U. S. Geol. Surv., Monogr. 52, pp. 1–641.

Vaughan, T. W.

1900. The Eocene and Lower Oligocene coral faunas of the United States. U. S. Geol. Surv., Monogr. 39, pp. 1–262, pls. 1–24.

Vokes, H. E.

1939. Molluscan faunas of the Domengine and Arroyo Hondo formations of the California Eocene. Ann. New York Acad. Sci., 38:1–246, pls. 1–22.

Vredenburg, E. W.

1906. The classification of the Tertiary system in Sind with reference to the zonal distribution of Eocene Echinoidea. Rec. Geol. Surv. India, 34:172–198.

Waagen, W.

1879–1895. Salt Range fossils. Palaeontologica Indica., ser. 13, 1(1):1–72, pls. 1–6; 2(1):1–323, pls. 1–40.

Wachsmuth, C., and F. Springer

1897. The North American Crinoidea Camerata. Mem. Mus. Comp. Zool., Vols. 20–21. 897 pp., 83 pls.

Walch, J. I.

1768–1771. Naturgeschichte der Versteinerungen, zur Erläuterung der Knorr'schen Sammlung. 3 vols. Nuremberg.

Walcott, C. D.

1898. Fossil Medusae. U. S. Geol. Surv., Monogr. 30. 369 pp., 33 pls.

1912. Cambrian Brachiopoda. U. S. Geol. Surv., Monogr. 51. 872 pp., 104 pls.

Weed, W. H., and L. V. Pirsson

1896. Geology of the Castle Mountain mining district [Mont.]. U. S. Geol. Surv. Bull. 139, pp. 1–164, maps.

Weed, W. H.

1899. Description of the Fort Benton Quadrangle [Mont.]. U. S. Geol. Surv., Geol. Atlas, Fort Benton. Fol. A (no. 55). 7 pp., maps.

1899. Description of the Little Belt Mountains Quadrangle [Mont.]. U. S. Geol. Surv., Geol. Atlas, Little Belt Mountains. Fol. (no. 56). 9 pp., maps.

Weller, Stuart

1914. The Mississippian brachiopoda of the Mississippi Valley Basin. Ill. Geol. Surv., Monogr. 1, pp. 1–508, pls. 1–83.

Whiteaves, J. F.

1876–1903. Mesozoic Fossils. Vol. 1, 416 pp., 51 pls. Geol. Surv. Canada, Ottawa.

Williams, H. S.

1895. Geological Biology. 395 pp. New York: Henry Holt and Co.

Williamson, W. C.

1858. On the Recent Foraminifera of Great Britain. 107 pp., 7 pls. London.

Willis, Bailey

1932. Isthmian Links. Bull. Geol. Soc. Amer., 43:917–952.

Windhausen, A.

1918. The problem of the Cretaceous-Tertiary boundary in South America and the stratigraphic position of the San Jorge formation in Patagonia. Amer. Journ. Sci., ser. 4, 45:1–53.

Wood, H.

1899–1913. A monograph of the Cretaceous Lamellibranchiata of England. 2 vols. Paleont. Soc. London.

Wood, S. V.

1848–1882. A Monograph of the Crag Mollusca. 4 vols., suppl. Paleont. Soc. London.

1861–1877. Monograph of the Eocene Bivalves of England. 1 vol. with suppls., 1–182, 1–24 pp., pls. 1–25, A, B. Paleont. Soc. London.

Woodring, W. P.

1925. Miocene Molluscs from Bowden, Jamaica. Pt. 1, Pelecypods and Scaphopods. Carnegie Inst. Wash. Publ. 366, pp. 1–222, pls. 1–28.

1928. Miocene mollusca from Bowden, Jamaica. Pt. 2, Gastropods. *Ibid.* Publ. 385, pp. 3–541, pls. 1–40.

Wright, Thomas

1878–1885. Monograph of the Lias Ammonites. 1–503 pp., pls. 1–78. Palaeont. Soc. London.

Zittel, K. A. von

1868. Die Cephalopoden der Stramberger Schichten, . . . Palaeontologische Mitt. Mus. K. Bayer. Staates. Vol. 2, abt. 1, pp. 1–118, atlas. Stuttgart.

1877–1878. Studien über fossile Spongien. Abh. K. Bayer. Akad. (Math.-phys. Kl.) Munich, 13:1–154, pls 1–9.

PLANT GEOGRAPHY

By RONALD GOOD
University College, Hull, Yorkshire

So intimately is the history of man related to the distribution of plants that it is scarcely an exaggeration to suggest that the study of plant geography must have begun with the first dawnings of man's consciousness of the potentialities of his environment, but today most botanists are content to claim for it a history of more comprehensible length. Some date its beginning from the days of Tournefort, who flourished about 1700 and to whom is attributed the first recognition of latitudinal and altitudinal zonation and the way in which these are the reflection of one another. Others call attention to Linnaeus' classification of plant habitats—his *Stationes Plantarum*—in the *Amoenitates*. The commonest practice, however, is to regard von Humboldt, the great German naturalist, as the father of plant geography. His travels in South America in the opening years of the nineteenth century resulted in one of the first scientific descriptions of equatorial vegetation, and the recognition of his fundamental contribution (von Humboldt, 1817). Humboldt has the merit of emphasizing that the first chapter of this science was, as it has been in so many others, essentially one of exploration and description.

In another sense, also, von Humboldt is a notable landmark. He is the connecting link between the great voyages of geographical exploration in the latter half of the eighteenth century, among which those of Captain Cook are so prominent, and the series of great scientific expeditions which may be considered to have begun with the voyage of the *Beagle* from 1831 to 1836. In view of the great distinction of Charles Darwin's subsequent studies in botany one cannot but regret, on reading his account of this voyage, that he was not then more concerned with plants. His preoccupation at that time with geology and zoology, an emphasis which later had such profound consequences, is evident, and it was not until a few years later, when the young Joseph Hooker set out in the *Erebus* on a voyage lasting from 1839 to 1843, that a real botanical milestone was reached.

It is not easy now to realize that these two series of expeditions—the great voyages of geographical adventure on the one hand and the great scientific explorations initiated by the voyage of the *Beagle* on the other—were in fact separated by little more than half a century for they seem to belong to different ages. True, these years had been memorable ones and had witnessed the vast liberating forces of which the American War of Independence and the French Revolution were expressions, yet even this does not adequately account for the difference of outlook that distinguished the second quarter of the nineteenth century from the third quarter of the eighteenth. It seems clear enough that there must have been in the latter period a tremendous intellectual leaven at work which was destined in the space of a comparatively few years to lighten the whole body of biological thought. This leaven may be described as the growing consciousness, not yet expressed in words but evidently present in the minds of many people, that the uninspiring doctrines of biological immutability must soon give way to something more in tune with the spirit of the times and, it may be added, more in accord with a rapidly growing body of observed facts. The spark that ultimately fired this tamped charge was, of course, the appearance of Darwin's *The Origin of Species* in 1859, but it is easy to see now not only that the fuse had been smouldering for years, but that the study of plant geography had made no small contribution to this result.

Indeed, it may be said with truth that, from the point of view of this subject, the foundation of the California Academy of Sciences in 1853 could scarcely have been at a more auspicious time, for it was followed within the short space of seven years by a series of publications which became classic and which, together, raised the subject of plant geography to a position of special importance and significance. First came Hooker's essay on the New Zealand flora (1853), to be followed two years later by A. L. P. P. de Candolle's *Géographie Botanique Raisonnée* (1855), which still remains one of the most considerable of all such works. Then, almost together, came Asa Gray's study of the flora of Japan (1859), the *Origin* itself (1859), and Hooker's second essay, on the flora of Tasmania (1859).

Looking back now in the light of so much after-knowledge it is difficult to recapture the intellectual atmosphere of the earlier eighteen-fifties, when the scientific world was so much smaller than it is now. Such recapture is particularly difficult when based on much of the contemporary literature. De Candolle's book is an instance of this. Here is a closely packed study of his subject of more than a thousand pages, of which the headings might serve almost equally well for a survey of similar scope today and in which the author comments with judgment on almost every aspect of the subject, and yet it is written entirely in what can today only be called the restricted idiom of pre-evolution. Even mutability is admitted, and there are discussed, more than once, the changes which species may come to suffer with the passage of time. But there the curtain falls, and one may search in vain for any recognition of the possibility that what may in due course befall species may itself be the origin of others. It is a remarkable example of scientific thought restrained by dogma.

De Candolle's book is in many ways a striking example of one written years before its time. It not only discusses many subjects the potentialities of which are really only now being tested, such as the order of families in floras or the proportions between monocotyledons and dicotyledons, but, as has been said, it discusses the circumstances surrounding the hypothetical creation of species with considerable acumen. So much emphasis is placed on this aspect of his subject that one almost inevitably wonders whether the author's major premise, which is the supernatural creation of species, can have been more than a piece of traditionalism designed perhaps to ensure that the rest of his work would not be dismissed too summarily. But this does not appear to have been the case. Thistleton-Dyer (1893), in his obituary of de Candolle, suggests that it was partly the influence of ideas about the climatic factors of distribution and partly a somewhat unimaginative quality of mind that made him miss the essential point by so narrow a margin. How near he had been to it he himself fully realized later, and it is pleasant to notice in after correspondence Darwin's great opinion of the *Géographie Botanique Raisonnée* and his appreciation of its author's generous attitude toward his own theories.

Asa Gray's relation to the story of the *Origin* is different. He was one of the few confidants whom Darwin had kept informed of the gradual development of his own theoretical opinions about evolution. Indeed, one of his frequent letters to Gray, which happened to express some of his ideas particularly concisely and conveniently (as well as to date them), was included as part of the joint communication of Darwin and Wallace to the Linnean Society of London by which the theory of natural selection was launched on July 1, 1858. The exact relation of Gray's classic paper on the North American and Japanese floras to the *Origin* is not simple to gauge now. This relationship was the subject of correspondence between the two authors during the preparation of Darwin's great work for the press, and it seems fair to regard Gray's paper as having been written in a form intended to provide possible additional evidence for Darwin's views. On the other hand Gray's formal attitude toward these views of Darwin's was one of studied caution. Although Darwin considered Gray one of his most valuable supporters, this support was tempered by a certain criticism because, it would seem, Gray felt that a judicial attitude of this kind would be more effective aid in the long run than any more spectacular and enthusiastic championing.

Hooker's two great papers were rather more profound phytogeographical studies but are perhaps to be thought of as less intimately involved with the trend toward evolution. They were obviously of great importance to it, since the facts that they set forth spoke for themselvess in no uncertain voice. Of course Hooker was even more closely associated with Darwin than was Gray but, to use an apposite simile, the work of the two seems to illustrate convergence rather than strict homology. It is perhaps an interesting commentary on this point that Hooker, at any rate from 1850 to 1856, repeatedly expressed pessimistic opinions about the progress and future of botany as a science, which suggests that he was not altogether fully conscious of how rapidly the renaissance was approaching. Let us hope that some of the pessimisms of today are equally ill-founded.

However, we must not allow ourselves to wander farther down the by-ways of evolutionary history, fascinating though these are. What has been outlined has been intended to illustrate how opportune the founding of the Academy was and to call attention to the three great botanists, de Candolle, Gray, and Hooker, who dominated the phytogeographical scene at that time. There is nevertheless one other point about this birthday which must not be overlooked here, namely, that it occurred only three years after California had become a state of the Union. This surely is but further evidence, if such were needed, of that intellectual leaven to which reference has already been made.

With the coming of evolution the whole meaning of plant geography altered. It has often been said that the real evidence of the truth of the theory of evolution lies, not in this or that array of facts, but in its power as an organizing concept. Without it, the facts appear chaotic; with it, they fall into order to a remarkable degree. Nowhere is this more true than in plant geography, which is so fundamentally a mass of descriptive fact, and this is one of the reasons why it became to the evolutionists one of the most promising and popular aspects of botany. The other and even more important reason was the recognition, under the new conception, of the inevitable relation between time, space, and change. All this meant that the world vegetation and its distribution, which previously had been, as it has been expressed, matters for wonder but not for speculation, could now be, and indeed had to be, restudied from the point of view of the new theory, and a vast new field thus opened. Plant geography had, in short, to be translated into the new idiom. In this way the whole subject developed so quickly that only the most prominent features of its history can be noticed in one short paper.

It is very obvious from a study of botanical literature in general that the characteristics of different nations and peoples express themselves as much in their methods of scientific inquiry and in their predilection for certain aspects of their subjects as they do in many other ways. A philosopher could probably explain convincingly why it was that the German school of botanists almost at once made the newly opened fields so particularly their own, quickly reaching in them a preeminence which they maintained for many years. If an explanation is to be hazarded here, it is that this next phase of the subject was necessarily one of bringing some sort of order out of an enormous and rapidly accumulating mass of data, and that this was work which called for just those qualities of application, industry, and organization that are such strong German national features.

The first, and in some ways the greatest, of these German publications was Grisebach's *Vegetation der Erde* (1884), which first appeared in 1871, then in an enlarged edition in 1884. This may almost be described as the first full-scale attempt to give a coherent single description of the vegetation of the whole world and to classify it floristically, and the best compliment that can be paid it is to say that it is still an extremely valuable source of basic information. Indeed, the most striking thing about it now is how little it has been rendered obsolete by subsequent increase in our knowledge, and one can only be surprised that so authoritative and complete an account could be prepared at that comparatively early date. Actually, as the preface to the first edition says, the book is a synthesis of studies extending over thirty-five years, and thus is partly pre-Darwinian, as is evidenced by the stress laid on temperature as a distributional factor. This emphasis derives from de Candolle, and is partly Darwinian, as is shown by its clear expression of the evolutionary conception of adaptation to environment. It must also be borne in mind that this book dates from a time when the distinction between floristic and vegetational studies had scarcely begun to be made, and it would perhaps be fairer to regard it as an early essay in what later became distinguished as plant ecology (it contains, for instance, one of the first classifications of growth form), though it also includes much direct information about the spatial distribution of plants. A contemporary study more definitely developmental in outlook was the briefer early work of Engler which is often referred to as the *Versuch* (1872–1882).

The mention of Engler, who was, within the scope of his interests, one of the greatest of all German botanists, brings to mind another gradual divergence of subjects such as is inevitable with the passage of time and the growth of material. The study of plant geography must always rest largely on the devoted work of the taxonomists. In earlier days the two fields were almost parts of one whole, but later taxonomy came to absorb nearly all the energies of its chief practitioners. This is true of both Hooker and Engler, whose careers have many interesting parallels. Each was early attracted by geographical problems and retained his interest in these throughout his long life. But both later devoted themselves especially to systematics, Hooker's work in this field culminating (in collaboration with Bentham) in the *Genera Plantarum* (1862–1883) and in a number of floras, of which that of British India is preeminent (1875–1897), Engler's work in his well-known *Syllabus* (11th ed., 1936), and in the editing of such great undertakings as the *Natürlichen Pflanzenfamilien* (Engler and Prantl, 1889–1924) and *Das Pflanzenreich* (Engler, 1900). Much the same is true, too, of de Candolle, whose energies were later deeply absorbed in the continuance of his father's *Prodromus* (A. P. and A. L. P. P. de Candolle, 1824–1873).

Drude was perhaps in the more direct geographical succession, and in particular will always be remembered for his *Atlas der Pflanzenverbreitung.* This was published in 1887 as part of a larger physical atlas and consisted of a short series of excellently produced maps showing the ranges of various important plant elements, both vegetational and floristic, accompanied by a concise explanatory letterpress. The work of Drude, however, is more generally known from his *Handbuch der Pflanzengeographie,* which appeared in 1890 and contained among other things an improved floristic classification. This, however, though an important book, said little that was entirely new and gives the impression rather of belonging to the end of an epoch.

It is very noticeable, in the gradual development of a science, how often progress takes the form of successive pulsations, each giving great impetus to the study for a time but then tending to lose momentum, being replaced in due course by some new intensification along some rather different line. Thus it would seem that by the eighteen-nineties the forward urge provided by Darwinism had begun to work itself out and that some new impulse was due. This came in the form of a concentration upon the relation between the plant and its immediate environment or habitat, a new approach or point of view to which was given the name "plant ecology," or "oecology," as it was first spelled. The first principles of this new discipline, which, as we shall see, has since become the sister of the older plant geography in the stricter sense, were set forth in two books which were, effectively, more or less contemporaneous. These were Warming's *Plantesamfund,* published in Denmark in 1895 and later translated into the more familiar *Oecology of Plants,* and Schimper's *Pflanzen-Geographie auf Physiologische Grundlage* (1898), which also was translated into English some years later.

There is no doubt that a powerful influence in the hiving off of plant ecology was the reaction against the aridity which had affected much of botany through an overemphasis on formal morphology. It may be said to have been based on two fundamental propositions: that the plant itself is a living organism in close and intimate relation, both functionally and structurally, with the conditions of its environment, and that vegetation is a dynamic complex expressing the same laws of universal change with time as everything else in nature. Schimper himself expressed this idea (loc. cit.) when he said that the problems of plant geography will not be exhausted when the world flora is completely known (a contingency which, strangely enough, he seems to have thought imminent) but will become of a rather different sort and particularly concerned with the explanations of the differences between floras in different parts of the world.

For vegetation is always developing; floras occupy only a moment of vegetational history; and it is the relation of structure, function, and environment which must be studied.

It was very early recognized that plant geography is a matter which involves, in a peculiarly direct way, the fundamental conceptions of both space and time, and that the subject might, therefore, be approached from one or other of these directions or from some combination of both. Thus there has always been in plant geography an underlying triplicity; the swing of emphasis within this provides the background to the history of the subject. Just how the three streams or branches of plant geography should be defined and named has been a matter of considerable argument. Those who are interested in terminologies will find excellent accounts of this by Rübel (1927) and by Wulff (1943), but it is more convenient here to describe this triplicity in rather freer terms. First, there is the stream in which the main emphasis is the correlation of space and form; this has been the special concern of those plant geographers, like de Candolle, Hooker, Asa Gray, and Engler, who have also been preeminent systematists. It may be called the taxonomic stream. Second, there is the stream in which the strongest emphasis is placed upon the historical and developmental aspects of the subject, and this is perhaps most often now called the historical stream. Third, there is the stream in which the two conceptions of space and time are balanced more evenly than in either of the others, namely ecology, which is mainly concerned with the distributional changes, usually by their nature relatively small, resulting from the gradual changes in a mutable environment.

The main point in relation to this analysis is very clear: the coming of Darwinism shifted the emphasis away from the first stream, where it had in fact been almost wholly concentrated, and distributed it more evenly among all three. For a good many years the full effect of this was not felt because this was a period of reorientation, but once this adjustment had been made, the rapid development of the streams which had been so long held back by the pre-evolutionary conception of the cosmas was inevitable. For reasons which we need not attempt to specify too closely but which are certainly connected with the full flowering of the idea of adaptation to environment the ecological stream was the first to break through.

So simple an analysis is likely to be too clear-cut to depict the whole truth, and this is certainly so here, especially with regard to the first two streams, between which there has always been a close connection. We may indeed recognize two streams, but there is, as it were, a constant interchange of water between them. The ecological stream, however, has much more noticeably scoured its own channel and, although this stream flows alongside the others, there is little actual communication between them. The reasons for this would make a most interesting study, for they are probably not all purely botanical, but this is no place to attempt it. We must content ourselves with the statement that what is now called plant ecology became in a comparatively short time largely divorced from the other aspects of plant geography. There is therefore both reason and excuse for referring only briefly to it here, apart from the fact that, since ecology was unknown as a separate study in 1853, it may formally be considered outside the terms of present reference.

It is difficult to mark the exact point at which plant ecology became established as a separate subject, but it is not unreasonable to think of Schimper's *Pflanzen-Geographie* as belonging to the older dispensation and of Warming's *Plantesamfund* as belonging to the new, though in fact this is the reverse of their actual dates of appearance. Apart from these two it was perhaps the work of Flahault, of Montpellier, rather than that of any other man that gave the initial impulse to ecology, which at first consisted largely of the mapping of vegetation, such as he had been doing in France for some years. At all events it was one of his pupils, Robert Smith, who introduced his methods into Britain. But shortly after this Smith unfortunately died and, although his work was carried on by his brother and others, it later met with practical difficulties. Attention then passed, largely under the leadership of Tansley, happily still with us, rather to the analysis of vegetation and the study of the different kinds of plant communities, work in which a very definite stage was reached by the publication in 1911 of Tansley's *Types of British Vegetation.*

As might be assumed, a similar and indeed even greater development had been taking place synchronously on the continent of Europe, in which indeed so many names claim recognition that it is almost invidious to make a selection. Among the significant works the following stand out clearly: Schröter's publication (with Früh) of *Die Moore der Schweiz* (1904), which was a landmark; Raunkiär's classic study of growth form (1907); and Rübel's later work, *Pflanzengesellschaften der Erde* (1930), which is a remarkable study of European plant communities. According to Tansley (1911) Schröter also deserves mention as the first to distinguish between "synecology," or the study of plant communities in relation to their habitats, and "autecology," or the study of the ecology of single species.

In America the growth of the new subject went hand in hand with that in the Old World, as instanced by Hitchcock's *Oecological Plant Geography of Kansas* (1898) and by the *Phytogeography of Nebraska* by Pounds and Clements (1900), but with a rather greater emphasis on the developmental aspects. By 1899 Cowles had begun to publish on the subject of plant succession, the great later expansion of which under the leadership of Clements (1916) is one of the notable features of American plant ecology. It is interesting to note this difference of emphasis for it is surely indicative of the great distinction between European and American ecological development. European botanists had, of necessity, to work upon a vegetation which could be considered natural only by a considerable exercise of imagination, whereas the American school had as its subject vast areas of country over which the influence of man had scarcely been felt at all. It is not surprising in this circumstance that American ecology developed very rapidly and, in many directions, soon attained a leading position.

Although it has been convenient to regard plant ecology as stemming from Schimper and Warming, it needs to be stressed that this really marks the formal separation of the subject—its coming of age—rather than its birth, for these were certainly not the first publications written from the ecological standpoint. There were, for instance, the studies of Graebner (1895) and others on the North German heaths in the earlier 'nineties; and, especially, Drude's account in 1890 of the plant formations of Central Europe, which actually incorporated some forms of later ecological nomenclature. Earlier still, in the 'eighties, there were Krasnov's account of some of the Russian steppes (1886), Sargent's report on the North American forests (1884), and Christ's book on the Swiss vegetation (1879). Indeed, from almost the earliest days there had been a slowly increasing concern with ecological problems in plant geography, until shortly before the first World War the literature of ecology had grown so great that it became desirable to establish special periodicals to accommodate it, a stage it which we may perhaps consider the subject to have passed, for the time being at least, beyond the purview of this paper.

The end of the nineteenth century marked also the centenary of the departure of von Humboldt and Bonpland on their travels in tropical America. Readers will find an interesting account of the development of plant geography up to 1900 in Engler's contribution to the Centenary volume of the Berlin Geographical Society (1899), in which he first traces the beginnings of the subject from the earliest times and then its gradual growth on the floristic side, region by region.

The double deflection, or apparent deflection, of interest which followed the turn of the century, on the one hand toward more narrowly taxonomic work and on the other toward ecology, for a time left the middle stream of plant geography a somewhat feeble one. In this direction, at any rate, the fifteen years or so preceding the war were not among the most remarkable. This diversionary tendency was intensified also by one of the most considerable advances of that time, the growth of the subject of genetics, for, as will be seen, it was not until considerably later that the underlying unity between genetics and plant geography became perfectly realized.

Nevertheless these years were far from being entirely barren. In particular the German school continued to demonstrate its leadership in its chosen fields by the continuation or launching of such great projects as Engler and Drude's *Die Vegetation der Erde* (1896—)—among the volumes of which Harshberger's *Phytographical Survey of North America* is conspicuous—and Karsten and Schenk's *Vegetationsbilder* (1903—) which presents so much of interest and importance in the international language of illustration; by such books as those of Solms-Laubach (1905) and Schröter (1912); and by innumerable shorter publications, notably in Engler's *Botanische Jahrbücher*. Most of these are on the border line between historical and taxonomic plant geography, but an important direct contribution to the former was the comparison by Engler of the floras of tropical Africa and of tropical America, a subject which was later to become much more topical.

In addition, these years saw the earlier writings of several whose major contributions to plant geography were to come after the war, among them Fernald, Merrill, Skottsberg, and Willis, but one of the most important series of writings came from H. B. Guppy. Guppy was not a biologist by professional training except in so far as he began his career as a naval surgeon, but he was that much rarer thing, a born naturalist and observer, and he made good use of the fortune which took him for many years to what are some of the most interesting parts of the world from the point of view of plant geography. His larger works, namely, *Observations of a Naturalist in the Pacific* (1903–1906), *Studies in Seeds and Fruits* (1912), and *Plants, Seeds and Currents in the West Indies and the Azores* (1917), are perhaps a little voluminous and prolix for ordinary reading but they are unquestionably the work of a mind possessed of unusual descriptive and analytical powers. The second volume of the first-mentioned work, which deals with plant dispersal, will long remain a classic source of fact and commentary on that subject and its many related problems. Rather later on, and partly in association with Willis, Guppy turned his attention toward historical plant geography, and two of his papers in this field, *The Island and the Continent* (1919), and *Plant Distribution from the Standpoint of an Idealist* (1917–1920), are notable for their penetration and freshness of thought.

Again, although the prewar years may not have been very eventful scientifically, it was in this period that the foundations were laid for much of the later progress, especially in the increase of knowledge during the years in two fields relating to the distant past. First, it was a time of great activity in paleobotany, and although the more spectacular expressions of this centered in epochs too remote to interest the phanerogamist, it produced many important studies on fossil angiosperms. Among these the earlier works of Berry in America (e.g., 1911) and the studies of the Reids in England (e.g., 1908) may be specially noted, the one adding to our knowledge at the earlier end of the angiosperm time scale, the other at the later end. Second, there was a great development in the study of glaciation and its possible consequences, particularly as regards the Pleistocene. It may be claimed that our modern conceptions on this subject date from these years, which saw the publication of Penck and Brückner's *Die Alpen in Eiszeitalter* (1901–1909), as well as much of the work of Andersson, de Geer, and others.

This is perhaps the most appropriate point also for a brief reference to the study of the distribution of cryptogamic plant groups. Because the spermatophytes reproduce by what are usually macroscopic seeds, because they generally have bulky and resistant plant bodies, and because they have a relatively short geological history, their plant geography has particular values of its own which must not be applied to other groups, though each group has its own relation to this subject. Unfortunately, for the lower plants, much less of the necessary background knowledge is available and the practical difficulties are greater; thus it is fair to say that the only groups of cryptogams which have received the same kind of geographical treatment as the seed plants are the easily collected groups of the ferns and mosses. Christ's standard work on ferns, the *Geographie der Farne* (1910) dates from these prewar years, but the main work of this period, Herzog's *Geographie der Moose,* was rather later (1926). Most groups have of course received incidental treatment in the course of taxonomic studies, as for instance in the two editions of the *Pflanzenfamilien,* but, apart from those mentioned, the only plants which need comment are the lichens, another easily collected group, some of which have long attracted attention by reason of their extraordinarily wide ranges. Indeed, crytogamic phytogeography is largely an untilled field, but it is also one with special difficulties of its own, chiefly inherent in the much longer and more hazy geological history of these plants.

About the time of the first World War another switch of emphasis became apparent. As already explained, Schimper had long since pointed out that existing floras exhibit only one moment in the history of the earth's vegetation and that in consequence the history of the earth's surface is a matter which must deeply concern the plant geographer. About 1915 several circumstances conspired to focus attention on this aspect of the subject, so that what had in fact always been its core became crystallized more definitely than hitherto into what has now become known as historical plant geography. Among these circumstances was certainly the normal swing of the pendulum, in this case from the extreme of formal taxonomy and purely descriptive ecology. Two other not clearly related influences, however, were more particularly concerned. These were the publication by Willis (1922) of his theory of age and area and the publication by Wegener (1924) of his theory of continental displacement.

There is much evidence for the belief that the success of a scientific theory has often been due to the fact that a general combination of trends and circumstances, not in themselves easily discernible, have served to predispose public opinion favorably toward it, almost as if an unconscious sort of propaganda had been at work. There is little doubt, for instance, that this is broadly true of Darwinism itself, which, when the time was fully ripe, became widely established with what was really remarkable rapidity and unanimity. So with the two theories just mentioned. They were something new when the times were set for novelty and because of this, and also perhaps because each contained an element of the mysterious, they gained considerable attention.

Willis' work appeared straightforwardly as a contribution to botanical thought, but it developed from an evolutionary approach to the subject. Readers may find elsewhere (e.g., New Phytol. [1951], 50: 135) accounts of it longer than is appropriate here. It need only be said that Willis was attracted to the subject of plant geography mainly because of the way in which it seemed to him capable of helping toward a better understanding of the processes of organic evolution and particularly because of the way it might be made to afford evidence against the theory of natural selection, which Willis' experience caused him to criticize. Very briefly, Willis maintained that the choice lay between natural selection and mutation and that, since mutation requires no assumption of a widespread supersession and elimination of "unfit" species, which is inherent in the conception of natural selection, any detection of an exponential rate of speciation and spread might be held to indicate that mutation rather than selection had been the paramount process in evolution. Such an exponential rate Willis claimed to demonstrate in the "hollow curve" type of graph. As a projection of this, as it were, Willis argued that under continuous mutation, not only would the totality of species constantly increase, but, barring accidents, the longer a species existed the wider would be its spread, and it is by this conception of "age and area," as he called it, that his scientific work is most familiar.

This is not the place to attempt an appraisal of Willis' theories or an assessment of his direct contribution to plant geography as such. His claim to a place in the history of that subject is based on something rather different, for the service that he rendered was that of provoking (to use the *mot juste*) a renewed interest in the whole science. But this does not altogether explain the almost violent reaction that many of his opinions occasioned and there were, it seems, two other reasons. One certainly was that he had the temerity to question the long popular theory of natural selection; the other, that he puts into words what many felt. For both these different reasons his writings received a measure of publicity and criticism which possibly surprised no one more than their author.

As we now look back through the years, the nature of Willis' achievement in plant geography has become clearer. It is that he showed, even if without first intent, that plant geography was not the exhausted subject which had yielded place to more modern disciplines but was a living one which still posed profound problems of fundamental importance. In short, he did much to restore to it the prestige which, during the previous generation, it had seemed to lose; and it is important to realize this because it helps to relate his work to that which we must now go on to notice.

Wegener's theory of continental displacement, or "drift" as it is sometimes called, dates from about 1915, though it did not become common currency until after the war, and its basic conception was not altogether novel. The relation between ideas of continental displacement and plant geography is a double one. First, the facts of discontinuity or disjunction, using those terms in their widest sense, clearly provide some circumstantial evidence for or against the view that displacement may have occurred; second, the idea is valuable to those who would explain the floristic relationships which today exist between the separate continental masses. Both aspects combine to make drift a particularly live problem for plant geographers.

Up to the present, and despite an enormous amount of study from various points of view, ideas of continental movement remain hypothetical. No summing up of the matter is really possible, but the situation in relation to the geography of the flowering plants, as it stands today, can be stated quite shortly. For at least one hundred years—which means in effect ever since the subject of plant geography took real form—there has been a common belief that the leading facts cannot be explained at all satisfactorily so long as it is held that the geography of the world, and particularly the isolation of the continents, has always been as it is now. In this connection it is well to remember that there are two ways in which a junction may be effected between separated entities. One is by interposing something in such manner as to bridge the gap between them; the other is by moving one or other of them bodily until the two come into contact. The first method, since it did no violence to generally accepted beliefs, was for long the accepted explanation; but it has aspects which, purely from the point of view of the plant geographer, make it a less attractive proposition than the second. As for the more direct geological and other evidences for displacement, these are at present generally held to be inadequate, and those who favor this theory are therefore faced with the fact that, on this ground, it is not generally acceptable to geologists and geodesists. How far this essentially negative attitude of objection is justified time alone will show; but there are not a few who feel that the rejection of a hypothesis simply on the ground of inexplicability is unwise. Finally, with regard to Wegener's theory it must not be forgotten that it involved not only continental displacement, but also the idea of a more or less continuous movement of the poles. Any such movement would of course in turn involve corresponding movements in the climatic zones of the world, and a possibility of this kind as an explanation of many difficult phytogeographical facts has scarcely been sufficiently examined as yet.

Early in the interwar years there came two important developments which derived directly from the earlier work on glaciation already mentioned. The more important was the growth, under the leadership of Erdtman (1943) and others, of the technique of pollen analysis. This technique made it possible to form various postulates from the proportionate occurrence of different kinds of pollen grains in peat and similar deposits about the nature of the vegetation contemporary with the deposits and thus to draw a much more complete picture of the general conditions of the time. Strictly, pollen analysis is on the borders of plant geography, especially where that subject impinges on archaeology, but within its limitations it has been and doubtless will continue to be a valuable adjunct.

The second development was the discussion which grew up around what is usually called the "nunatak theory," the view that some elements of the preglacial floras survived those ages on refuges actually within the ice-cap but not themselves glaciated. This idea again was not in itself new, but in the nineteen-twenties it received much fresh impetus from the explorations of Fernald in the region of the St. Lawrence River, and from his energetic writings (e.g., 1925). The general suggestion of which this was a particular expression is an attractive one, namely, that the explanation of certain puzzling phytogeographical facts is to be found in the occurrence of refuges where plants may have been able to avoid the worst consequences of climatic change and survive. But there is as yet no overwhelming evidence that it is necessary to invoke this explanation.

The last few paragraphs deal with matters which, despite their apparent diversity, nevertheless have a considerable common element, revealing clearly the main trend in the study of plant geography between the two wars, namely, its concentration on the historical-developmental aspects of the subject. Major works in this tradition soon appeared, and price of place may be given to Irmscher's *Pflanzenverbreitung und Entwicklung der Kontinente*, published in 1922 and followed in 1926 by Hayek's *Allgemeine Pflanzengeographie*, which, although much more of a textbook, had the same approach. Both of these are important, but it is fair to regard a later book as the real primer of the new interest. This was Wulff's *An Introduction to Historical Plant Geography* (1943), which was composed much more in the new idiom than either of the earlier books. This publication is important, too, as marking the entry into the field of the great new Russian school of botanists which had grown up since the Revolution, a school whose full influence is still impeded by barriers of alphabet and language. Fortunately Wulff's first volume, which was published in 1932, was translated into English during the war, but his second and much larger volume is still available only in Russian. This is also true of the monumental *Flora URSS* edited by Komarov, begun in 1934 and still in active progress. It contains a great mass of information about the distribution of plants over the huge but hitherto little studied tracts of much of central and eastern Asia.

This is perhaps the best place at which, ignoring chronology for the moment, to refer briefly to two later publications, because, with that of Wulff, just mentioned, they form a mutually complementary trilogy, covering with reasonable adequacy most aspects of modern plant geography and giving as complete a picture of the present situation as can, in all circumstances, be expected. These are Cain's *Foundations of Plant Geography*, which appeared in 1944, and the present writer's book, *The Geography of the Flowering Plants*, written before the late war but unavoidably delayed in production until 1947. Both have historical plant geography as their chief emphasis, but while the former is of special interest for its treatment of many particular aspects of the relation between evolution and plant geography, such as polyploidy, the latter is rather more a review of the facts of angiosperm distribution and a reconsideration, from a developmental point of view, of the factors which have caused them. All three of these books take, at least as a partial basis, the theory of tolerance, published in 1931, by the author of the last of them in an attempt to integrate into some generally applicable working hypothesis of plant geography the many "factors of distribution."

Returning now to a more general consideration of the interwar years we find that the literature of plant geography is so extensive that it is difficult to select from it, though several broad features demand comment. One of these is the special attention given, notably by German workers, to the more detailed study and analysis of types of distribution area, or areography as it has come to be called, a subject to which Hannig and Winkler's new serial publication *Die Pflanzenareale,* founded in 1926, contributed much and of which there have been various minor reflections in more recent years. Another noteworthy and valuable feature of this period was the large number of memoirs written about various phytogeographically strategic parts of the world by authors fully conversant with their floras. Anything like an exhaustive list would be much too long here, but they may be exemplified by the work of several authors: Allan and Oliver for New Zealand; Bews for South Africa; Perrier de la Bathie for Madagascar; Gleason for the mountains of southern Venezuela; Guillaumin and others for New Caledonia; Setchell and many others for various parts of the Pacific; Scottsberg and St. John for Hawaii; Skottsberg for Juan Fernandez; Lam and van Steenis for parts of Malaysia; Merrill for the Philippines, and Hultén for the region of the Bering Strait.

With all this went many advances in cognate subjects, as, for instance, the study of angiosperm fossil floras in which the work of Berry and, rather later, Chaney was notable, but for the rest it must suffice to mention, as representative of many others, three books which, though very different from one another, nevertheless each added something of worth to the general store. The first of these, in order of appearance, was Marcel Hardy's little book *The Geography of Plants* (1925), the uninspired title of which may well have served to obscure its very real merit as one of the few really concise and readable general accounts of world vegetation as a whole. The second is the volume of essays published in honor of W. A. Setchell (Goodspeed, ed., 1930) in which a number of eminent phytogeographers give authoritative accounts of their own special interests. The third is Ridley's great book *The Dispersal of Plants Throughout the World* (1930), in which there is surely gathered together all that is known, or at least was known at that time, about this peculiarly bewildering subject. Probably no other branch of plant geography has been so misunderstood, and even so much misrepresented, as this, and Ridley, although he confines himself largely to the recording of facts, at least provides some kind of sheet anchor, so that the subject may be more safely approached.

Of the years since the outbreak of the second World War not much can be said here. They are too close to allow us to generalize and it can only be said that the literature is still copious and shows no sign of abatement. One or two items of this period have already been referred to and to these a few others must be added. Two publications of the actual war years testify to the continued vitality of what has been called here the German school, namely, three papers by Vester (e.g., 1940), in which he summarizes, with the help of small maps, the distributions of all the families of angiosperms, and Meusel's book *Vergleichende*

Arealkunde (1943), which is in many respects a textbook of areography. More recent is the great Dutch project of the *Flora Malesiana* (van Steenis, ed., 1948—), which, although in the main taxonomic, is so broadly based on geographical principles that it can scarcely fail to add enormously to our knowledge of the distribution of plants in a particularly significant part of the world. There are also numerous accounts of the phytogeography of sundry parts of the northern temperate regions and to represent these there can be no better choice than Hultén's beautifully produced *Atlas* (1950), which deals exhaustively with the geography of the Scandinavian flora. Of very different scope is Willis' third and largest book *The Birth and Spread of Plants* (1949) which, somewhat hidden by a rather awkward kind of presentation, contains much of real importance.

The war itself was responsible for not a little progress in the paths of plant geography. The extension of hostilities into the great and relatively unfamiliar spaces of the Pacific, especially, caused a considerable revision and augmentation of our knowledge of those regions, in which the botanists took their fair share, as is instanced by Merrill's useful and delightful account (1946) of tropical vegetation in that area.

But the over-all impression of these later years, and one indeed hopes that it is a true estimate, is that there is coming about a much needed reintegration of the different branches of plant geography. This may be illustrated by reference to three points. First there is the growing tendency for purely taxonomic works, such as floras and systematic monographs, to pay more attention to the geography of their subjects, to bring together as much geographical information as they are able to and often to illustrate it with maps. This is desirable enough in itself, but it is also an enormous help to the phytogeographer, who must rely so much on reliable taxonomy for the facts which he endeavors to interpret. Second, one has only to look at recent volumes of the periodicals devoted to ecology to see how much the horizons of the ecologists have widened and how much more concerned with the main stream of plant geography they are becoming. Finally, there is the development which, more than anything else perhaps, characterizes the postwar years, namely, the growth of that combination of taxonomy, geography, and genetics which has come to be known as cytogeography, itself so essentially a synthetic effect. It is very apposite, in this volume which celebrates the first hundred years of the California Academy of Sciences, to mention a publication which best typifies this latest phase in the development of plant geography, Babcock's great study of the genus *Crepis,* which appeared in 1947. It is further work of this kind, based on phytogeographically significant plant groups, that is more likely than almost anything else to speed the progress of plant geography.

At the end of the first century of the Academy's history, what are the chief impressions? Two seem particularly noteworthy. One is the truth of the aphorism, *Plus ça change, plus c'est le même chose.* Probably no previous hundred years has seen such profound changes as this latest century, certainly not in the scientific world, and yet one cannot help feeling that, if Alphonse de Candolle and some of the other pioneers of plant geography could once more walk the earth, they would understand us and our problems pretty well, though we might for a time speak in rather different dialects. Advance in knowledge since their time has indeed been enormous, but it has been amplification rather than violent change, evolution rather than revolution. There have been secessions, but there have also been federations, and the main outlines of the subject now are very much what they were a hundred years ago. The difference is that we have a deeper understanding of them.

A second impression, or so it seems to the present writer, is that today, just as in 1853, we stand on the threshold of great advances in biological thought and method. Our particular subject, plant geography, involves the former rather than the latter, but the indications of future change are not far to seek. There is an increasing impatience with ideas which owe their perpetuation more to tradition than to logic, and for many there is a growing doubt of our ability to arrive at the answers of some of our most urgent problems with our present major postulates. It is easy enough, one realizes, to forecast change when there is no obligation to foretell its shape, but its prognostication may at least help us to be ready for it and to take advantage of it.

To this end there are two aids. The first is austerity, or perhaps asceticism is a better word, in scientific thought and theory. Today the pressure of events and many other influences combine to make more than ever difficult the pursuit of truth for its own sake, and it must not be forgotten that this is the only real road to scientific progress. There is need too for a higher standard of logical argument and a stronger guard against facile generalizations and false conclusions. The second requisite is receptiveness and suppleness of mind which, it is perhaps worth stressing, is in no way antipathetic to intellectual integrity. Every new idea, however fantastic it may appear at first sight, is entitled to critical consideration, and the wise man will treat none with complete contempt. It has been well said that all great truths begin as heresies and that all new knowledge contradicts the old. However true this dictum may or may not be, it is at any rate an admirable motto for the study wall of the plant geographer.

BIBLIOGRAPHY

BABCOCK, E. B.

1947. The Genus *Crepis*. Pt. I. The Taxonomy, Phylogeny, Distribution, and Evolution of *Crepis*. Univ. Calif. Publ. Bot., 21. xii + 197 pp. Berkeley and Los Angeles.

BENTHAM, G., and J. D. HOOKER

1862–1883. Genera Plantarum. 1(1862–1867); 2(1873–1876); 3(1883). London: Reeve and Co.

BERRY, E. W.

1911. The Lower Cretaceous Flora of the World. *In* Maryland Geol. Surv., 1896—Cretaceous . . . 1911, pp. 99–151.

CAIN, S. A.

1944. Foundations of plant geography. 556 pp. New York: Harper.

CANDOLLE, A. L. P. P. DE

1855. Géographie Botanique Raisonnée. Vol. I, xxxii + 606 pp.; Vol. II, 607–1365 pp. Paris: V. Masson.

CANDOLLE, A. P. and A. L. P. P. DE

1824–1873. Prodomus Systematis Naturalis Regni Vegetabilis. 17 vols. Paris: Treutel et Würtz.

Christ, H.

1879. Das Pflanzenleben der Schweiz. xiv + 488 pp. Zürich: F. Schulthess.

1910. Die Geographie der Farne. 357 pp. Jena: G. Fischer.

Clements, F. E.

1916. Plant Succession. Carnegie Inst. Wash. Publ. No. 242. 512 pp. Washington.

Cowles, H. C.

1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot. Gaz., 27:95–116, 167–202, 281–308, 361–391.

Darwin, Charles

1859. The Origin of Species by Means of Natural Selection. 6th ed., 1881. 434 pp. London: Watts.

Drude, O.

1887. Atlas der Pflanzenverbreitung. 6 pp., 8 maps. Gotha: J. Perthes.

1890a. Handbuch der Pflanzengeographie. 582 pp. Stuttgart: J. Engelhorn.

1890b. Vegetationsformationen erläutert an der centraleuropäischen Flora. Bot. Jahrb. Engler, 11:21–51.

Engler, A.

1879–1882. Versuch einer Entwickelungsgeschichte der Pflanzenwelt. I, 202 pp.; II, 347 pp. Leipzig: Engelmann.

1899. Die Entwickelung der Pflanzengeographie in den letzten hundert Jahren und weitere Aufgaben derselben. *In* Wiss. Beitr. z. Gedächtniss der hundertjährigen Wiederkehr des Antritts v. A. v. Humboldt's Reise nach Amerika, 1799. Ges. Erdkunde. 247 pp. Berlin: W. H. Kühl.

1900– (Ed.) Das Pflanzenreich. 105 vols. Leipzig: W. Engelmann.

1905. Ueber floristische Verwandschaft zwischen dem tropischen Afrika und Amerika, sowie über die Annahme eines versunkenen brasilianisch-Äthiopischen Continents. Sitzungsber. K. Preuss. Akad. Wissen. Berlin, 1905(6):180–231.

Engler, A., and O. Drude (eds.)

1896–1928. Die Vegetation der Erde. 1st and 2d eds. 15 vols. Leipzig: W. Engelmann.

Engler, A., and L. Diels

1936. A. Engler's Syllabus der Pflanzenfamilien. 11th ed. xiii + 419 pp., 476 figs. Berlin: Gebr. Borntraeger.

Engler, A., and K. Prantl

1889–1924. Die natürlichen Pflanzenfamilien. 1st ed., 1889–1915; 2d ed., 1924– . Leipzig: W. Engelmann.

Erdtman, G.

1943. An Introduction to Pollen Analysis. 239 pp. Waltham, Mass.: Chronica Botanica.

Fernald, M. L.

1925. Persistence of plants in unglaciated areas of boreal America. Amer. Acad. Arts and Sci. Mem., 15:241–342.

Good, R.

1931. A theory of plant geography. New Phytol., 30:149–171.

1947. The Geography of the Flowering Plants. 403 pp. London and New York: Longmans, Green.

Goodspeed, T. H. (ed.)

1936. Essays in Geobotany in Honor of William Albert Setchell. xxvi + 320 pp. Berkeley: Univ. Calif. Press.

Graebner, P.

1895. Studien über die norddeutsche Heide. Bot. Jahrb. Engler, 20:500–654.

Gray, A.

1859. Diagnostic characters of new species of phaenogamous plants, collected in Japan by Charles Wright, with observations upon the relationship of Japanese flora to that of North America, and other parts of the north temperate zone. Amer. Acad. Arts and Sci. Mem., n.s., 6:377–452.

Grisebach, A. H. R.

1884–1885. Die Vegetation der Erde nach ihrer klimatischen Anordnung. 2d ed. Vol. 1, 567 pp.; Vol. 2, 594 pp. Leipzig: W. Engelmann.

Guppy, H. B.

1903–1906. Observations of a Naturalist in the Pacific between 1896 and 1899. Vol. 1 (1903), Vanua Levu, Fiji, xix + 392 pp.; Vol. 2, Plant Dispersal, xxvi + 627 pp., 5 pls., 5 maps. London and New York: Macmillan.

1912. Studies in Seeds and Fruits. 528 pp. London: Williams and Norgate.

1917. Plants, Seeds and Currents in the West Indies and the Azores. 531 pp. London: Williams and Norgate.

1917–1920. Plant distribution from the standpoint of an idealist. Journ. Linn. Soc. Bot., London, 44:439–471.

1919. The island and the continent. Journ. Ecol., 7:1–4.

Hannig, E., and H. Winkler (eds.)

1926– Die Pflanzenareale. 5 vols., Vol. 2 with L. Diels; Vol. 3 with G. Samuelsson; Vol. 5, maps. Jena: G. Fischer.

Hardy, M.

1920. The Geography of Plants. 327 pp. Oxford: Clarendon Press.

Harshberger, J. W.

1911. Phytogeographical Survey of North America. lxiii + 790 pp. New York: Stechert and Company.

Hayek, A.

1926. Allgemeine Pflanzengeographie. 409 pp. Berlin: Gebr. Borntraeger.

Herzog, T.

1926. Geographie der Moose. 439 pp. Jena: G. Fischer.

Hitchcock, A. S.

1898. Oecological plant geography of Kansas. Acad. Sci. St. Louis. Trans., 8:55–69.

Hooker, J. D.

1853. Introductory Essay to the Flora of New Zealand. London.

1859. On the Flora of Australia, its Origin, Affinities and Distribution; being an Introductory Essay to the Flora of Tasmania. 128 pp. London: L. Reeve.

1875–1897. The Flora of British India. 7 vols., in 24 parts (1872–1897). London: Reeve and Co.

Hultén, E.

1950. Atlas över Växternas Utbredning i Fanerogamer och Ormbeinksväxter Norden. 512 pp. Stockholm: Generalstabens.

Humboldt, A. von

1817. De Distributione Geographica Plantarum, Secundum Coeli Temperiem et Altitudinem Montium Prolegomena. 249 pp. Paris.

Irmscher, E.

1922. Pflanzenverbreitung und Entwickelung der Kontinente. Studien zur genetischen Pflanzengeographie. Hamburg Inst. Allgem. Bot. Mitteil., 5:17–235.

KARSTEN, G., and H. SCHENK (eds.)
1904–1944. Vegetationsbilder. 26 vols. Jena: G. Fischer.

KOMAROV, V. L. (ed.)
1934–1952. Flora URSS. 18 vols. Moscow and Leningrad: The URSS Acad. Sci. Press.
1941. Materials on the History of the Flora and Vegetation of the URSS. Fàsc. I. 413 pp. Moscow and Leningrad: The URSS Acad. Sci. Press. (English summaries of Russian papers.)

KRASNOV, A.
1886. Geobotanical researches in the Kalmuk steppe. Russ. Geog. Soc. St. Petersb. Bull., 22:1–52.

MERRILL, E. D.
1946. Plant Life of the Pacific World. 295 pp. New York: Macmillan.

MEUSEL, H.
1943. Vergleichende Arealkunde. 2 vols., Vol. 1, 437 pp. Berlin: Gebr. Borntraeger.

PENCK, A., and E. BRÜCKNER
1901–1909. Die Alpen in Eiszeitalter. 3 vols. Leipzig: C. H. Tauchnitz.

POUND, R., and F. E. CLEMENTS
1900. The Phytogeography of Nebraska. 442 pp. 2d ed. University of Nebraska.

RAUNKIÄR, C.
1907. Planterigets Livsformer og deres Betydning for Geografien. 132 pp. Copenhagen.

REID, C., and E. M. REID
1908. On the pre-glacial flora of Britain. Journ. Linn. Soc. Bot., London, 38:206–227.

RIDLEY, H. N.
1930. The Dispersal of Plants throughout the World. 744 pp. Ashford, England.

RÜBEL, E.
1927. Ecology, plant geography and geobotany, their history and aim. Bot. Gaz., 84:428–439.
1930. Pflanzengesellschaften der Erde. 464 pp. Bern-Berlin.

SARGENT, C. S.
1884. Report on the forests of North America. 612 pp. Washington: Government Printing Office.

SCHIMPER, A. F. W.
1898. Pflanzen-Geographie auf physiologische Grundlage. (1903) 876 pp. (Eng. trans. by Groom and Balfour, 1903. Oxford.) Jena: G. Fischer.

SCHRÖTER, C.
1912. Genetische Pflanzengeographie. Jena.

SCHRÖTER, C., and J. FRÜH
1904. Die Moose der Schweiz. Berne.

SOLMS-LAUBACH, H.
1905. Die leitenden Gesichtspunkte einer allgemeinen Pflanzengeographie in kurzen Dorstellung. 243 pp. Leipzig: A. Fèlix.

STEENIS, C. G. G. J. VAN (ed.)
1950– Flora Malesiana. Djakarta: Noordhoff-Kolff.

Tansley, A. G.

1911. (Ed.) Types of British Vegetation. xx + 416 pp. Cambridge Univ. Press.

1947. The early history of modern plant ecology in Britain. Journ. Ecol., 35:130–137.

Thistelton-Dyer, W. T.

1893. Alphonse de Candolle. Nature, 48:269–271.

Vester, H.

1940. Die Areale und Arealtypen der Angiospermen-Familien. Bot. Archiv, 41:203–275, 92 figs.

Warming, J. E. B.

1895. Plantesamfund. vii + 335 pp. Copenhagen: P. G. Philipsen.

Wegener, A. L.

1924. The Origin of Continents and Oceans. (Eng. trans. from 3rd German ed. by J. G. A. Skerle.) xx + 212 pp. London: Methuen Co.

Willis, J. C.

1922. Age and Area. A Study in Geographical Distribution and Origin of Species. 259 pp. Cambridge: Univ. Press.

1949. The Birth and Spread of Plants. Geneva.

Wulff, E. V.

1943. An Introduction to Historical Plant Geography. (Eng. trans. by E. Brissenden.) 223 pp. Waltham, Mass., U. S. A.

ANIMAL GEOGRAPHY

By KARL P. SCHMIDT
Chicago Natural History Museum

The comprehensive work on the subject of Animal Geography, published in 1853 by Ludwig Schmarda, of the University of Gratz, serves very well as a summary of the state of knowledge in this field in the eighteen-fifties. *Die geographische Verbreitung der Thiere* devotes 93 pages (with no less than 129 pages of notes and references) to the modality and causality of animal distribution, in which he discusses the influences of heat, light, air, electricity, climate, seasonal cycles, and food, much as the ecological factors in animal distribution are set forth today. In this section it is apparent that the data were in every respect inadequate for a comprehensive review in 1850. Schmarda goes on to discuss the dependence of animals on their medium and substrate, the altitude distribution of both land and marine animals, general ideas about dispersal, and the concepts of faunas and zoological regions. He has taken the step, bold enough for 1853, of giving up the concept of a single center of creation and of dispersal in favor of a number of such centers. He is aware also of the phenomenon of vicariation, of the replacement of one species of animal by an obviously related one in adjacent areas or regions. His twenty-one terrestrial and ten marine regions are rather casually chosen and as casually characterized by some dominant group —the Middle European Realm, for example, is the realm of insectivores and of carabid and staphylinid beetles, Madagascar the realm of lemurs. The discussion of the terrestrial regions occupies 143 pages, with 258 pages of references, and that of the marine regions 58 pages with 94 pages of notes. A colored Mercator map delimits the 31 realms.

On the eve of the revolution in zoological thought brought about by Darwin's *Origin of Species,* the delimitation of the principal faunal regions of the world was the principal preoccupation of zoologists interested in distribution. Thus in 1858 P. L. Sclater set forth the principal terrestrial regions as indicated by birds, and in the same year Albert Günther did the same for reptiles, with a very fair agreement between the two distinct approaches.

The appearance of Darwin's *Origin of Species* in 1859 marked a radical change of direction and an enormous stimulus to botanical and zoological explorations and studies in every field. By Darwin's time, the broad patterns of animal distribution shown by the larger and otherwise more conspicuous animal types had been made known, and the existence of these patterns presented increasing difficulties to theories of special creation. Thus Darwin's summary of the evidences from animal distribution that favored the evolutionary origin of animal types (whether species, genera, or higher groups) marked the end of the purely descriptive era, and the beginning of a period of interpretation and speculation and re-examination of the phenomena in the field of geographic distribution of plant and animal life, as in all other segments of biology.

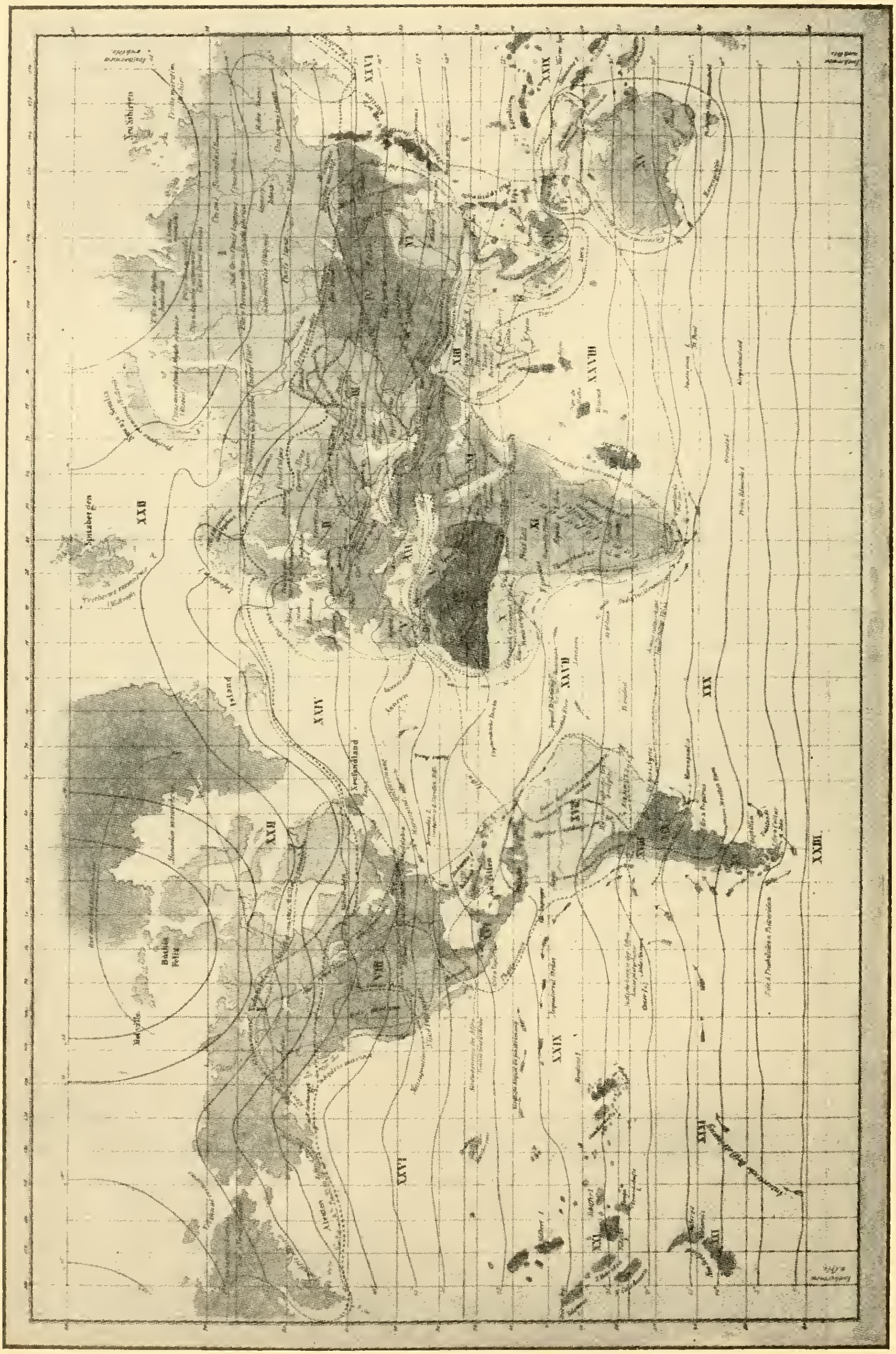


Figure 1. Schmarda's attempt to divide the world into zoological regions (see opposite page). From Schmarda, 1853.

Darwin had been strongly influenced in his whole evolutionary trend by the facts of animal and plant distribution. He devotes two chapters in the *Origin of Species* to this subject, and in these he discusses the genetic similarities within the faunas and floras of the several continents; the means of dispersal available to plants and animals; the influence of glacial periods on distribution; the distribution of freshwater animals; and the inhabitants of oceanic islands. In illustration of the last mentioned topic he deals especially with the animals and plants of the Galapagos Islands, where the phenomena of insular distribution had so greatly impressed him in 1835.

Alfred Russell Wallace, Darwin's friend and fellow evolutionist, had lived for many years in tropical regions, first in the Amazon Basin and later in the East Indies, where he had been especially impressed by the phenomena of animal distribution. He thus had a broader and more direct and intimate acquaintance with the subject than any other naturalist traveler of his century. He was continually at work on this subject from 1860 until 1876, the date of publication of his two volumes on *The Geographical Distribution of Animals.* He somewhat modestly refers to this work as an extension and amplification of the two chapters on the subject in the *Origin of Species,* comparing it with Darwin's own two-volume expansion of the chapters on animals and plants under domestication. The two principal sections of Wallace's work are contrasted as "zoological geography," a descriptive discussion of the land animals of the different zoogeographic regions, and "geographical zoology," a review of the distribution of vertebrates and certain invertebrates, group by group. This work was ponderous and at the same time naïve in supposing that "a solution of zoogeographic problems could be attempted with some prospect of success." It remains a necessary work to a specialist in this subject, but modern changes in classification, the great advances in paleontology, and the rise of ecology, combine to make it useless as an introduction to animal geography. The more popularly written *Island Life* (1880) is

---

Figure 1. General map of the geographic distribution of animals, drawn up by Ludwig K. Schmarda, 1852. The land realms are: I. the Arctic, realm of fur bearers and aquatic birds; II. Central Europe, realm of insectivores and staphilinid and carabid beetles; III. Caspian Steppe, realm of the saiga antelope and of burrowing rodents; IV. Central Asian Steppes, realm of the horse tribe; V. European Mediterranean, realm of heteromeran beetles; VI. China, realm of pheasants; VII. Japan, realm of the giant salamander; VIII. North America, realm of rodents, conirostrine and dentirostrine birds; IX. Sahara Desert, realm of the ostrich and of melasomas (tenebrionids); X. West Africa, realm of catarrhine monkeys and termites; XI. Highland Africa, realm of ruminants and pachyderms; XII. Madagascar, realm of lemurs; XIII. India, realm of carnivores and pigeons; XIV, the Sunda World, realm of snakes and bats; XV. Australia, realm of the marsupials, monotremes and meliphagid birds; XVI. Central America, realm of land crabs; XVII. Brazil, realm of edentates and platyrhine monkeys; XVIII. Andean, realm of the llama and condor; XIX. Pampa, realm of the viscacha and "harpalid" beetles; XX. Patagonia, realm of Darwin's rhea and of the guanaco; XXI: Polynesia, realm of nymphalid butterflies and of the Apteryx (New Zealand). The marine realms are: XXII. Arctic Ocean, realm of marine mammals and amphipod crustaceans; XXIII. Antarctic Ocean, realm of marine mammals and penguins; XXIV. North Atlantic Ocean, realm of cods and herrings; XXV. South European Mediterranean, realm of the labrid fishes; XXVI. North Pacific Ocean, realm of the scombrid and mail-cheeked fishes; XXVII, Tropical Atlantic Ocean, realm of plectognath fishes, manatees, and of pteropods; XXVIII, Indian Ocean, realm of buccinoids and hydroids; XXIX. Tropical Pacific Ocean, realm of corals and holothurians; XXX. South Atlantic Ocean; XXXI. South Pacific Ocean.

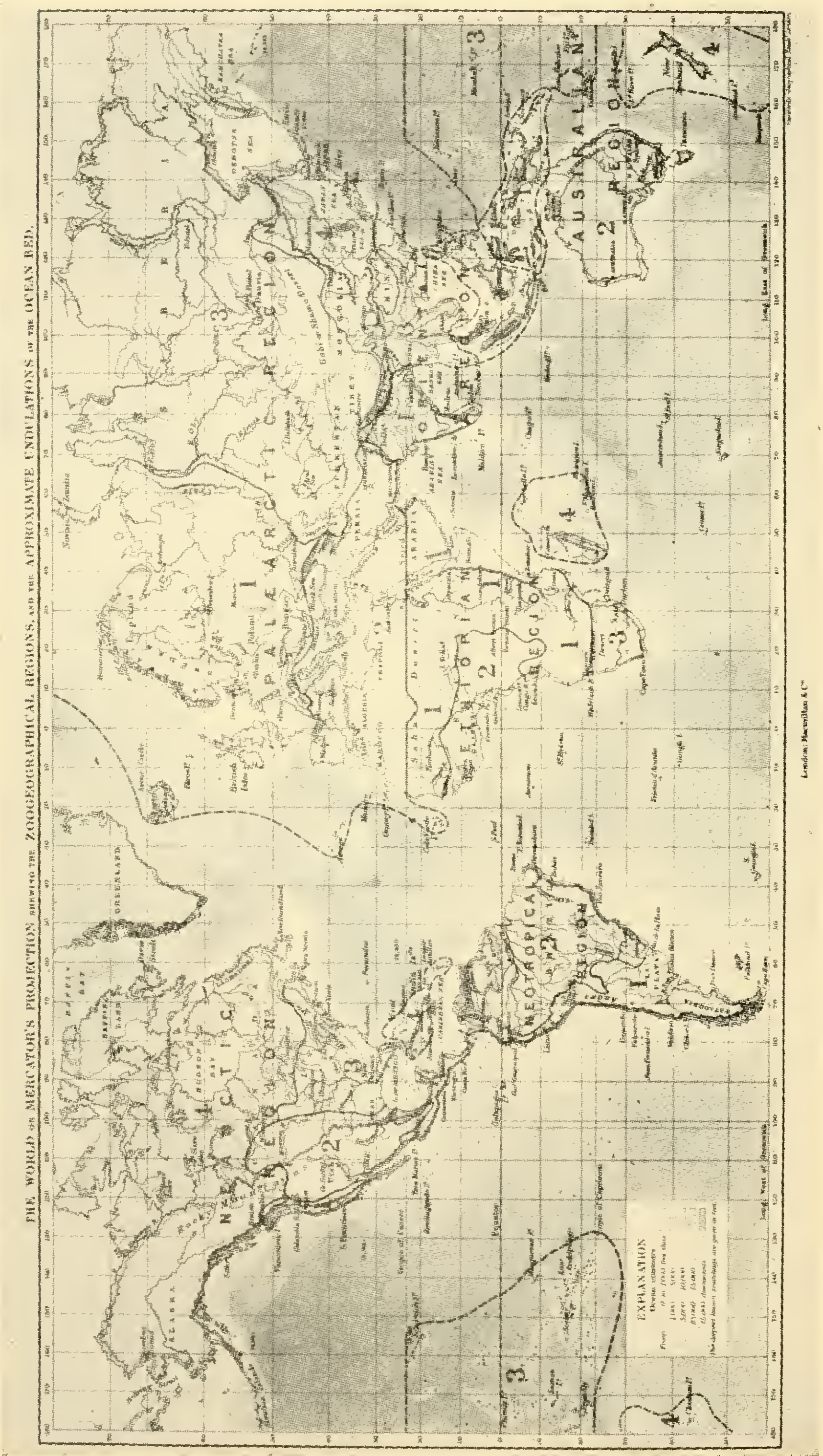


Figure 2. Wallace's zoogeographic regions. From Wallace, 1876.

Wallace at his best. Freed of much of the cumbrous and now obsolete detail that burdens the larger work, the later volume remains a satisfactory and vivid introduction to the study of animal distribution. Unfortunately the long and detailed discussion of the causes of glacial periods rather arbitrarily inserted in this work seems to a modern or skeptical reader incredibly optimistic in its over-simplification of so complex a subject. A completely revised edition of *Island Life,* retaining as much as possible of Wallace's own writing, is much to be desired.

In broad outline, the historical development of zoogeography is dominated by Wallace in the generation between the eighteen-fifties and the date of *Island Life.* This generation concerned itself with an accumulation of the facts of distribution in what might be called "Descriptive Animal Geography"; and with fundamental improvements in the classification of animals. The delimitation and classification of the geographic subdivisions of the earth's surface that seemed to accord best with the facts of animal distribution was perhaps the principal subject of controversy in this period, much of it based on inadequate studies or fields too limited to afford contributions of permanent value. Wallace had adopted the system of regions proposed by Sclater with only a few changes of names. Thomas H. Huxley's entry into the field in a well-reasoned paper on a limited group of birds (1868) must be mentioned, since it suggests an important reclassification and hierarchial arrangement of the zoological regions into three principal realms. An anonymous writer proposed acceptable terms for these—"Arctogaea," to include the Palearctic, Nearctic, Oriental, and Ethiopian regions; "Neogaea" for the Neotropical region; and "Notogaea" for the Australian. This, with the combination of the Nearctic and Palearctic regions into the Holarctic by Heilprin in 1878, leads directly to the modern grouping of realms, regions, subregions, and provinces.

For all the enthusiasm of Wallace, and in spite of the fact that he and his contemporaries quite correctly assessed the revolutionary importance of the theory of evolution to the concepts of animal geography, the era in which his *Geographic Distribution of Animals* was the leading work in the field remained essentially involved in these static problems. There was a long series of papers involving the problem of combining the Nearctic and Palearctic regions into an over-all Holarctic region; and whether a distinct Sonoran region should be cut off from the Holarctic to include the southern half of North America. The controversy as to where to draw the line between the Oriental region and the Australian, and especially as to the place of the fauna of Celebes in this scheme, became a zoogeographic classic, which has had renewed attention in the decade of the nineteen-forties. There was endless report and argument about the *degree* of relation between one faunal province and another based entirely on the *existing* faunas, without reference to their origin and history.

Permanence of Continents

Darwin and Wallace, with the American geologist Dana to support them, regarded the continents as stable features of the earth's surface, and postulated connections between the continents and between continents and islands only where they exist now, as at Panama; or where there are shallow seas, *within* *the limits of the continental platforms,* which drop off quite abruptly to the abyssal ocean floor at about the 200-meter depth line. Wallace accordingly framed the classification of islands into "oceanic" and "continental," the oceanic islands being thought to have received all of their plant and animal life overseas, whereas the continental islands were populated overland, by direct invasion.

The directly demonstrable land connections between continents, and between islands and continents, that have been available for the dispersal of land animals are few. There is the existing Central American isthmus connecting North and South America; the shallowness of Bering Sea and narrowness of Bering Strait indicate that this region afforded a broad connection of North America with Asia; and except for the man-made Suez Canal, Africa is connected with western Asia, and was much more broadly connected in the past before the block-faulting that produced the Red Sea. The past connection of the British Isles with the European mainland and of the Greater Sunda Islands (Borneo, Sumatra, and Java) with southeastern Asia are undoubted, documented physiographically by the drowned river valleys in the neighboring shallow seas.

Land Bridge Speculations

With these known connections to explain the existence of animal life in certain islands and to explain the resemblances and relations between animals of one continent and another, it was perhaps natural to turn to hypotheses of other transoceanic land connections to explain such facts as the predominance of marsupials in Australia and South America, or of certain types of freshwater fishes in Africa and South America. The trend to bold hypotheses of this kind begins with the English naturalist Edward Forbes, as early as 1846. Forbes analyzed the fauna of the British Isles as to its various components, and found an element in the south of England and Ireland related principally to the life of Spain and Portugal. To explain this relation, he supposed the former (but quite recent) existence of a continental land mass projecting far out into the Atlantic. At first thought, since it was known that the sea had widely transgressed most continental areas for long periods in the past, it seemed logical enough that land areas might equally as well have been present where the oceans now lie. Hypothetical continents or isthmuses—"land bridges"—between continents were proposed and drawn in upon maps, and presently received names. An "Atlantis" was thought to have occupied most of the North Atlantic, and an "Archhelenis" the South Atlantic. Antarctica was renamed as "Archinotis." "Lemuria," constructed to account for the distribution of lemurs, spread across the Indian Ocean from India and Ceylon to Madagascar. "Pacelia" was a lobe of hypothetical land connecting the Hawaiian Islands with North America.

Such speculations were strongly re-enforced by the geological hypothesis of a "Gondwana Land" uniting all of the southern continents in Paleozoic and much of the Mesozoic time introduced in 1860 by the French-American geologist Marcou for the Jurassic, modified by Neumayr (1883 and 1887), and by Suess (1885), who placed its origin in the Paleozoic. The Gondwana Land hypothesis was based on the distribution of the remarkable fossil fern *Glossopteris* of Permian age, and on attempts to delimit continental borders in earlier geologic ages in the light of evidence from marine fossils. The great work of Edward

Suess, *Das Antlitz der Erde* (in which Gondwana Land was first so named) laid off the earth's surface in broad and bold tectonic outlines. Suess' ideas received support from the most eminent of geologists, as in Neumayr's later editions of the *Erdgeschichte,* Emil Haug's *Traité de Géologie,* and in Britain from J. W. Gregory. With such notable geological precedent, any specialist on any group of animals felt free to explain disconnected distributions by hypotheses of tongues of land extending over any water barrier that might separate even the species of a single genus; and such hypotheses can only be described for the era between 1880 and 1915 as "untrammeled."

The bridges became ever more complicated—R. F. Scharff, for example, thought that eastern and western Australia had been connected with Antarctica by two separate land corridors. Tongues of land were thought to be of short duration, lasting just long enough for the author's purpose and not so long as to allow additional and confusing emigrations and counteremigrations to take place.

During the era of land-bridge speculation eminent specialists in various fields became proponents of this or that pattern of connection between the southern continents. The great botanist Joseph Dalton Hooker had been impressed with the relations of the plants of southern South America, New Zealand, and Tasmania in the course of his early exploring voyage with the *Erebus* and *Terror,* from 1839 to 1843. The remarkable and distinctive Araucarian pines found in southern South America and in the islands near New Zealand, and the antarctic beech *Nothofagus,* found in Chile, New Zealand, and Tasmania, present to botanists exactly the kind of geographic relations that had led zoologists to speculate about direct land connections across existing oceans. The Swiss zoologist Rütimeyer, in an essay on the origin of the animal life of Switzerland, published in 1867, makes the suggestion of the former existence of a vast Antarctic continent, connecting all of the southern continents and New Zealand, and this idea received support from T. H. Huxley in 1870. The Antarctic and Pacific continents then expand and contract in the minds of F. W. Hutton (1873), Theodore Gill (1875), Hermann von Ihering (1891), H. O. Forbes (1893), Charles Hedley (1895), H. F. Osborn (1900), and A. E. Ortman (1901).

All of this land-bridge history is essentially independent of the geological theories of a Gondwana Land. Ideas of land bridges were integrated with the ideas of zoogeographers by Theodor Arldt, in *Die Entwicklung der Kontinente und ihrer Lebewelt* in 1907 (2d ed., 1936–1938). There is a little popular summary of the subject by Hans Gadow, in *The Wanderings of Animals* (1913).

Throughout all of this era of "land-bridge building," a few zoogeographers held to the basic assumption of the permanence of the existing continents and the distinction between oceanic and continental islands. Darwin wrote skeptically about "those who make continents as easily as a cook makes pancakes." Against much polemical sniping, Wallace held firm to his original position. Georg Pfeffer, almost alone among malacologists, held out against the too easy explanations of direct and multiple land connections. Anton Handlirsch took up the polemic cudgels and showed how disgracefully superficial and how incredibly arbitrary and thoughtless had been the "creation" of land bridges. By mapping the hypothetical connecting land areas proposed by his colleagues, he showed that almost every bit of existing ocean bottom had been raised and lowered. As the fore-

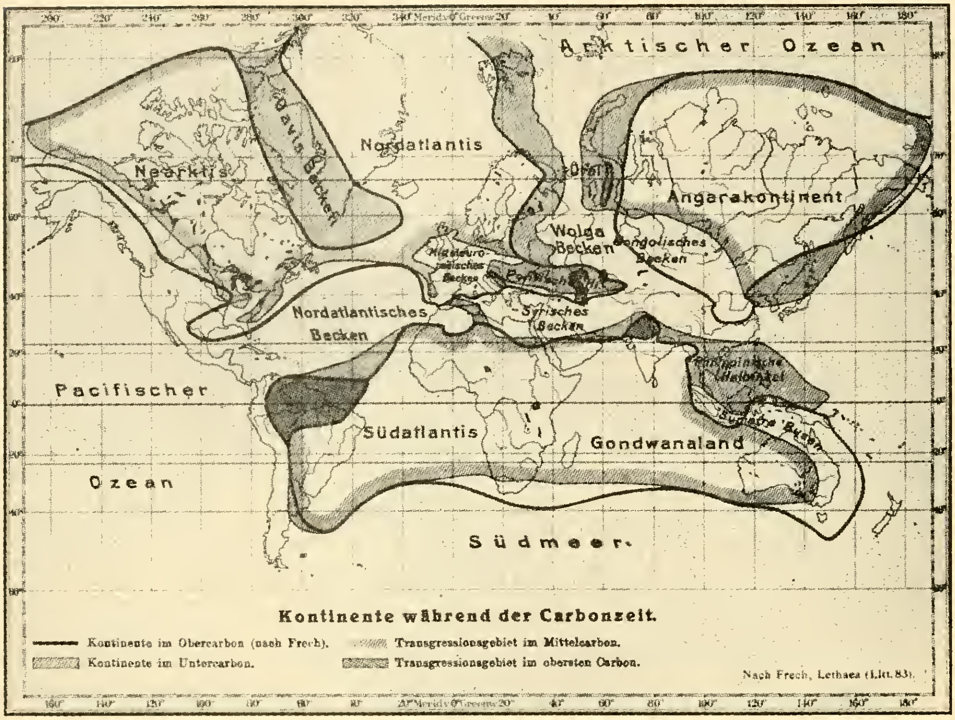


Figure 3. Land-bridges in Carboniferous and early Tertiary times, according to various authors. From Arldt, 1907.

most authority on fossil insects, Handlirsch analyzed the existing faunas of the continents and showed that even for this ancient and eminently terrestrial group the proposed connections of continents in the southern hemisphere are flatly opposed by a vast mass of contrary evidence. Only an uncritical enthusiasm could maintain them on faunal grounds alone; as we shall now see, there is crucial geological evidence against them.

Isostasy

The whole scheme of rising and sinking continents is now found to be opposed by unshakable geological evidence, from the facts summarized as "isostasy," which show that the continental platforms are indeed stable. The whole mass of books, journal articles, and addresses to scientific meetings on the subject of land connections is an incredibly futile chapter in the history of animal geography.

When the survey of the earth's surface had advanced to large-scale operations it was discovered that astronomical determinations of latitude were sharply at variance with direct measurement. The north-south breadth of Puerto Rico as found by astronomical calculation, for example, differs by about a mile from the 50-mile direct measurement. This difference results from a deflection of the plumb line toward mountain masses and toward continental masses. J. H. Pratt reported in 1855 "On the Attraction of the Himalaya Mountains and of the Elevated Regions Beyond Them Upon the Plumb Line in India." Since that time a gravity survey of the world has been made by means of the pendulum observations begun by George Biddell Airy at about the same time. The result of the world survey, which constitutes the science of geodesy, has been to re-enforce the validity of the principle of isostasy. It is found that the granitic materials of the mountains, the "sial" of Suess, have a density distinctly less than that of the basaltic rocks underlying the oceans, the "sima," in the proportion of 2.7 to 3.0. The sial, in a sense, floats on the heavier substratum of sima, and it is the sima that forms the ocean bottoms. The continental bases extend deep into the sima, with further great downward extending masses beneath the mountain ranges, except where their isostatic adjustment is not complete, as shown by the occurrence of earthquakes. An example of continuing isostatic adjustment familiar to us in North America is the rise of the northeastern quarter of the continent after the retreat of the continental glacier; the rare earthquakes in this otherwise extremely stable area are ascribable to the readjustment of the continental block with the disappearance of the ice load. The conviction that the continental platforms are indeed permanent in broad outline, and that the ocean floor is of very different composition, became more and more an axiom of modern geology as the extension of gravity measurements failed to find exceptions to the lightness of the continental masses relative to the ocean floors. This flatly contradicts the hypotheses of vast former continents extending across the existing oceans.

Continental Drift

Just when this began to be realized, an ingenious alternative was afforded by the hypothesis of continental drift elaborated by Alfred Wegener (1915), from ideas already current (Taylor, Baker).[1] Wegener, impressed by the current

1. Du Toit (1937) sketches the history of the ideas involved.

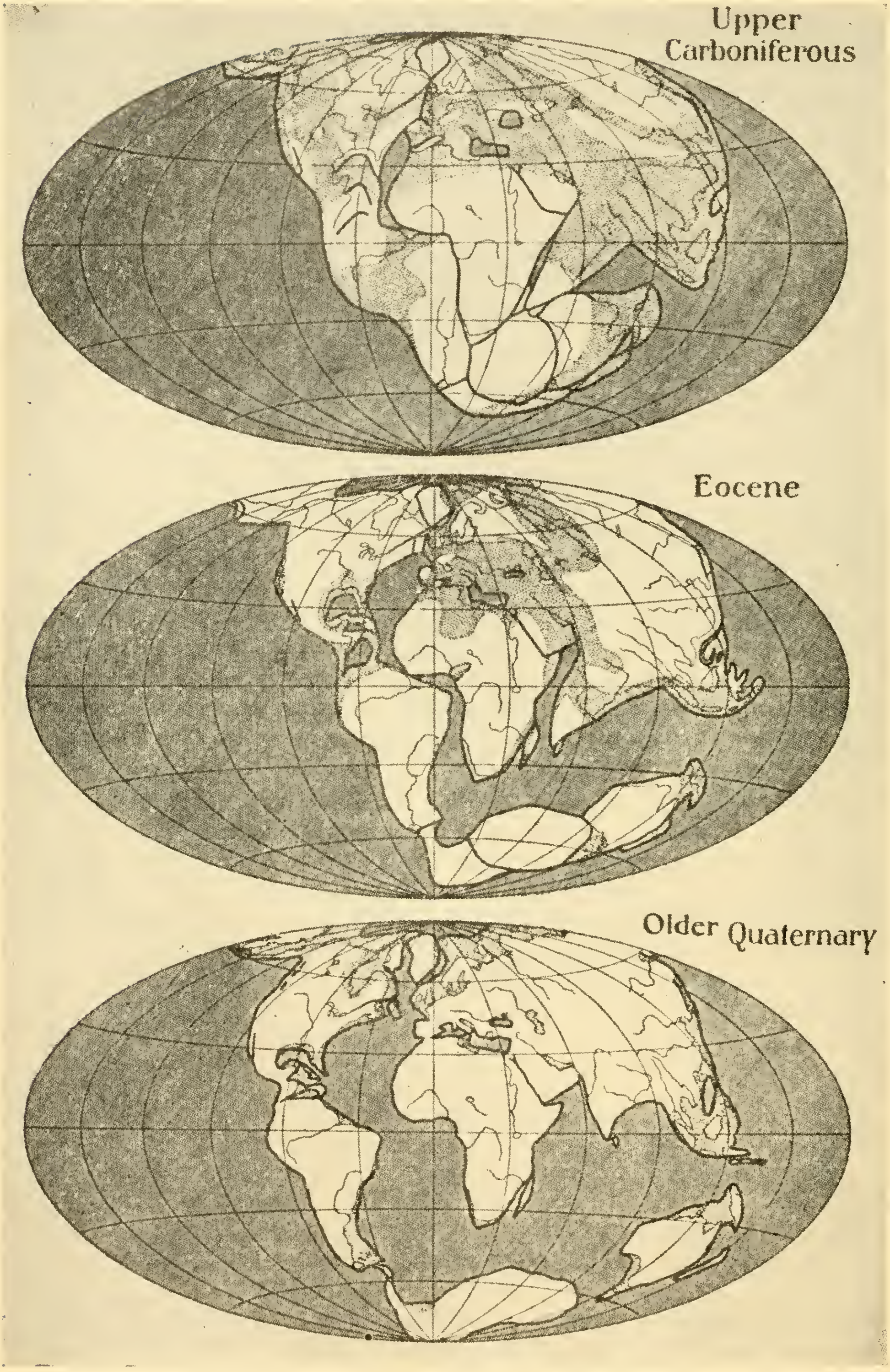


Figure 4. The arrangement of the continents in successive geological periods according to theories of continental drift. From various sources.

belief that continental connections are necessary to explain the existing pattern of animal life on the continents, suggested that the correspondence of the configuration of the Atlantic coast of South America with that of Africa was the result of a drifting apart of land masses formerly joined, and rent asunder in some past age. North America was thought to have drifted away from Europe in the same way. It was found possible to fit the Australian and Antarctic continents against South Africa, also, with the Indian Peninsula and Madagascar to fill the wedge-shaped gap between them, and to suppose that these land masses had drifted away from Africa to the south and east and north as the Americas had drifted to the west. The distribution of past continental glaciations and the distribution of Paleozoic coal deposits were brought into harmony with the theory of continental drift by assuming a different position of the poles during Paleozoic times. The actual break-up of the vast unified original continent is thought by Wegener and his school to have occurred at the end of the Paleozoic. Thus the theory is of little aid to those who had explained the distributions of relatively recent groups like the birds and mammals by means of land connections, or to those who invoked them for distributions of groups at the level of genera, which are demonstrably much more recent. To the more confirmed proponents of continental connections, however, this led merely to the outright belief that the continents had drifted back and forth—that they had been connected, separated, and reconnected.

The theory of continental drift has been received with considerable skepticism by American geologists, many of whom had had no prior belief in any continental connections other than those existing. The confirmation of the fact that the continents are in isostatic balance merely confirmed their ideas of the continents as vastly older than the life on them. In Europe a large group espoused the Wegnerian ideas, and the literature of the subject, and finally the literature of the controversy between drift and anti-drift proponents is now vast. Much of this literature, however, still assumes as axiomatic that a past connection of the continents is necessary to explain the present distribution of land life. In the very year when Wegener proposed his theory, this assumption was shown by William Diller Matthew to be invalid.

Climate and Evolution

The publication of Matthew's *Climate and Evolution* in 1915 was an event of primary importance in the field of animal geography. This paper sums up the accumulated paleontological evidence for the Tertiary distribution of mammals in a masterly way; it re-enforces the belief in the general permanence of continents, which had been a cardinal point with Wallace, but which had come to be more and more widely disregarded; it reverses a long accepted criterion for the place of origin of mammalian groups especially and of other animals in broad outline; and it offers a principal cause for the long-term dispersal of species, and of faunas with their environments, that links the subject of distribution with the whole course of evolution, and with a reasoned interpretation of the geological record. This work, in direct contradiction in many of its well-supported statements with the contemporary literature of animal geography, could not fail to have an extraordinary influence. A considerable number of subsequent distributional studies by students or disciples of Matthew have been based on Matthewsian principles; and the modern period in zoogeography must be dated from 1915. Matthew demonstrated that no hypotheses of trans-Pacific or trans-Atlantic connections between the continents are required to explain the existing distributions of mammals, and that the Mesozoic and Tertiary bridges between Asia and North America at Bering Strait and over the shallow Bering Sea, the Isthmus of Panama, with the perhaps still earlier bridge via the unstable island area between Australia and southeastern Asia, are the only continental connections for which valid evidence exists. This is documented from Matthew's unparalleled knowledge of mammalian paleontological history. As Darwin and Wallace and Handlirsch had rightly remarked, the axiom of general stability of the continents (to the outlines of the continental shelves) is essential to any orderly and critical investigation of animal distribution. Matthew could rest renewed affirmation of this axiom on the geological evidence for isostasy.

The more important contribution of *Climate and Evolution* is the presentation of an outline on the world scale, and in the grandest historical perspective, of the dispersal of land animals throughout geological history. This rests on the synthesis by Chamberlin and Moulton of the evidence from geological history as a whole for periodic cycles of great uplift of the continents with corresponding climatic extremes, diversity, and change, alternating with base-leveling by erosion ending in widespread uniformity and amelioration of climate. Matthew suggests that these large-scale changes have dominated progressive and adaptive evolution, and that ancestral types that failed to enter the main currents of evolution have either followed the climatic changes in their dispersal, to avoid the necessity of change, or have been forced by the competition of the advancing and physiologically more progressive types into geographically peripheral regions.

The examination of existing and fossil types at the peripheries of the ranges of their groups documents this broad pattern of dispersal. The continents of the southern hemisphere extend like vast peninsulas from the larger land masses of the northern hemisphere. It is demonstrable from the paleontological record that these larger northern land masses have been the main theaters of the evolution of mammals; and the southern continents are veritable museums of relict types preserved from past ages, whose ancestors are often known to have been present at earlier times in the northern hemisphere. Centers of origin are to be expected where the more advanced forms now live rather than where the most primitive forms are found.

Recognizing that the evidence from paleontology becomes progressively more obscure from the well-documented Tertiary history of the Age of Mammals through the Age of Reptiles in the Mesozoic to the origins of land animals in the Paleozoic, Matthew pleads for the interpretation of the less known by means of the better known, and doubts the existence of transoceanic connections of the southern continents even in the more remote geological periods. This is essentially the application of the "law of parsimony," which is basic to critical scientific thought.

The absurdity of Arldt's determination of the probability of past trans-Atlantic and trans-Pacific land connections by means of a statistical analysis of the "votes" of zoologists becomes evident after a critical examination of *Climate and Evolution.* This work disposes of the supposed necessity for such

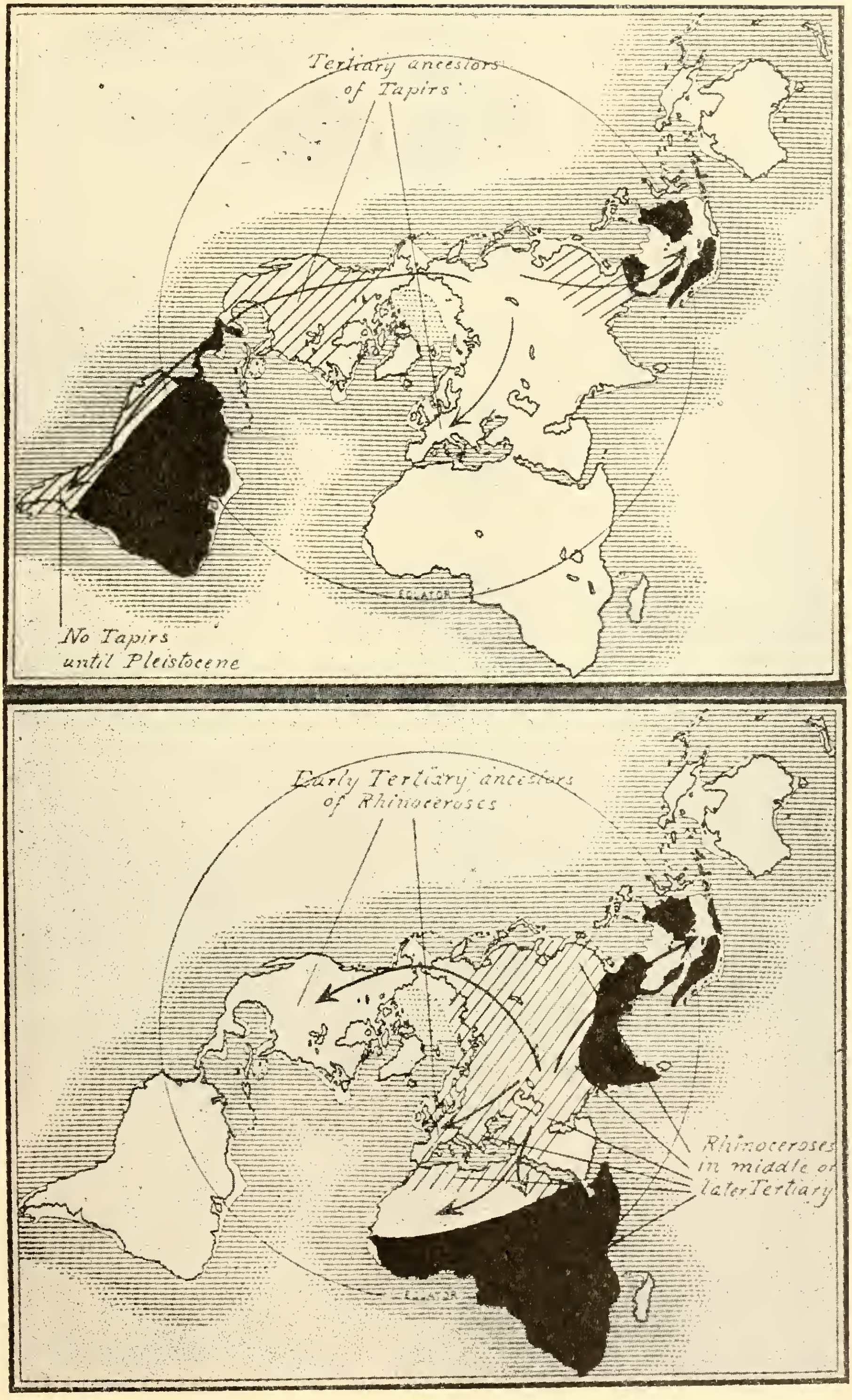


Figure 5. Matthew's maps showing origin and dispersal in geological time. Upper figure, the tapirs; lower figure, the rhinoceroses. From Matthew, 1915.

continental connections with much the same finality as did the *Origin of Species* for the necessity of the hypothesis of special creation. "Special Creation," in 1858, would have received an overwhelming majority vote from contemporary biologists.

A group of students in zoology and paleontology under William King Gregory at the American Museum of Natural History in the years 1915 to 1927 came also under the influence of W. D. Matthew, in whose personality great modesty and simplicity stood out against the background of an enormous scientific prestige. The group included Alfred Sherwood Romer, Charles Lewis Camp, and Gladwyn Kingsley Noble, with many others, and a little more indirectly Emmett Reid Dunn and myself. All of us have been involved in one way or another with the problems of animal geography, and all of us have remained disciples of Matthew. I was tempted to refer to my own commentary on Matthew (1943) as consisting of "Parerga and Paralipomena"; we have tended to look a bit askance at those "who knew not Matthew"; and it had not escaped some of our colleagues that Matthew's work had become a kind of Holy Writ to his disciples.

Fortunately we have now had a strong cross-light thrown on the main thesis of *Climate and Evolution* by a nondisciple, P. J. Darlington, Jr., of the Museum of Comparative Zoology at Harvard University, who reviews the whole matter from the evidence of the freshwater fishes, amphibians, and reptiles. These were the groups of which Matthew had least personal knowledge. Darlington shows that Matthew's account of these groups was quite inadequate and often erroneous, and that some of their major dispersals came from the tropics instead of from the northern continents; but he ends in essential agreement with Matthew in finding the Bering Sea and Bering Strait bridge adequate to explain the dispersals between the eastern and western hemispheres. The very important evidence of the freshwater fishes, long regarded as a proof of the necessity for past direct connection of Africa and South America, is now regarded by George S. Myers as explainable by long-term round-about emigration via the Bering Bridge rather than by hypothetical trans-Atlantic connections. Myers has more particularly analyzed the freshwater fish fauna of the West Indies (1938) and of Madagascar. He shows that the fish faunas of these two great island areas cannot possibly be interpreted on the theory of connection with the adjacent continents. He rejects any late Mesozoic land connection of Australia with southeastern Asia on account of the extreme impoverishment of the primary freshwater fish fauna of the Australian region (1951).

The important evidence from fossil plants has been presented and analyzed most recently by North American paleobotanists (Chaney, 1947). So far as the Cretaceous and Tertiary history is concerned, Chaney and Axelrod (to name only two) completely reject theories of land connection other than that at Bering Sea, and their account of the Tertiary history of the floras of the northern hemisphere is in essential agreement with Matthew.

One of the most striking relations between the recent faunas of South America and Africa lies in the rich, and in some respects parallel, development of the great group of worm-like lizards, the Amphisbaenidae. The group is wholly unknown in the modern fauna in eastern Asia. It is therefore especially illuminating that a fossil amphisbaenian of Oligocene age was discovered in Mongolia by the expedition of the American Museum of Natural History. It was described by Gilmore in 1943. This points again to the fact that the imperfections of the paleontological record must be borne in mind, and that closing its gaps must depend upon chance preservations as well as on chance discoveries.

A body of evidence bearing on the question of direct connection of Africa and South America, with much speculation derived from it, is supplied by the Permian reptiles of the order Mesosauria, and by certain members of the Triassic Rhynchocephalia, which are found in both continents. (See especially Edwin H. Colbert, 1952.) This finds support from the freshwater bivalves of the family Mutelidae, of which no fossils have been found in the northern hemisphere. Even in this case, the imperfections of the paleontological record and the possibility of convergence must be considered, for *Mycetopoda diluculi,* described in 1921 by Pilsbry, from the Triassic of Pennsylvania, may belong to this family.

The leadership among the group of Matthewsians has now somewhat naturally fallen to George Gaylord Simpson, who succeeded Matthew in the position of Curator in charge of Vertebrate Paleontology at the American Museum in 1944. Simpson had occasion to acquire the same kind of broad command of whole successions of extinct faunas. In a series of essays (1940–1952) he has dealt effectively with the difficulties of what appear as exceptional elements in these faunas —like the sudden appearance of the octodont rodents in South America, and the problems presented by the animal life of the West Indies and Madagascar. In 1945 he reviewed the whole classification of the mammals, living and extinct.

Later Land-Bridge Speculations

Matthew's reputation was so great among his close associates that it is disturbing to us to find him little recognized, or to find him even unknown in wide circles of geologists and geographers dealing with the problems of continental connections. Thus, in the face of isostasy, Charles Schuchert (1932) maintains connections from Madagascar to India, from Brazil to West Africa, and from Europe to Greenland. In an essay in the same year, with the title "Isthmian Links," Bailey Willis reduces the connections regarded as probable by Schuchert to narrow and sometimes tortuously crooked isthmuses, following the course of submarine ridges. Schuchert and Willis, on the geological side, thus stand solidly against the ideas of continental drift. Among botanists, one may cite W. H. Camp for his 1947 paper "Distribution Patterns in Modern Plants and the Problems of Ancient Dispersals." He thinks specifically in terms of Mesozoic east-west continent in the southern hemisphere, and more particularly of the origin of whole groups of flowering plants in the southern hemisphere. A European writer, Otto Wittmann, reviewing the problem in *Zoogeographica,* comes out flatly for a drifting back and forth of the continents (1934–1935).

The case of the *Hipparion* bridge, a hypothetical Miocene land connection from Florida to Spain, including the Antilles and North Africa, is an especially flagrant example of post-Matthewsian irresponsibility, for it not only fails to consider the contradicting evidence, but is itself based on conflicting and erroneous interpretations of the fossils involved. Proposed in 1919 by L. Joleaud as a solution of the existence of the horse-like *Hipparion* in Florida and Spain in Miocene times, it presently was cited to explain all kinds of mammalian faunal relations between the Old World and the New. By 1924 Joleaud had accepted the idea of continental drift as a necessary alternative to the idea of transoceanic bridges; but he then finds himself forced to elaborate the drift theory to that of an "accordion movement back and forth" of the continental areas. Equally oblivious of the problems introduced by land connection theories is the French entomologist René Jeannel, who believes in a mid-Tertiary connection of the Mediterranean region with the West Indies as necessary to account for the distribution of certain beetles (1935–1937) and later (1941) becomes a supporter of the ideas of continental drift as indicated by evidence from the faunas of the subantarctic islands like Kerguelen and the Crozets, as of continental drift in general from the viewpoint of entomology.

It is quite evident that there are still numerous believers in the former existence of continents where the great oceans now are; of movement of the continents to their present positions from an original single continent; and of back and forth movement of "accordion-type" continents. There is a strong opposing school of conservatives, who hold to the belief that the continental platforms, though obviously often flooded by epicontinental seas, have been stable throughout the geological ages in which life has existed on land. Much of this controversy is primarily geological, and only secondarily zoogeographic. My concern in this matter has been lest the geologists base arguments on those of zoogeographers and that these then complete an argument in a circle by triumphantly pointing to the fact that the geologists support them. If the geological theories involved were restricted to pre-Paleozoic or even to Paleozoic times, zoogeographers could have little to say regarding them.

Ecology and Animal Distribution

Historical animal geography becomes properly scientific only when there is adequate positive evidence from paleontology as to the history in question, and negative evidence is doubly to be discounted because the fossil record is in itself incomplete, while our exploration of the world for what fossils have been preserved is far from finished. The major factors producing disjunct distributions are the events of geological history, which are nonrecurrent. These can be reconstructed in convincing terms only when there is a quite exceptional wealth of fossil evidence. I have shown how wide is the divergence of opinion among zoogeographers in this field.

When we turn to contemporary animal distributions and examine them against the background of the existing environment, we enter a sharply contrasting realm of animal geography. Ecology, summing up existing environmental relations, supplies the guiding principles in our studies when we turn to the geography of existing forms, especially at the species and infra-species level, and equally when we attend to the minor biotic geographic subdivisions of a continent. A new hypothesis can be tested by further observation, or even by experiment, and the whole field is subject to steady and logical growth with the advance of knowledge. The problems directly involved become *ecological* instead of historical. We still must face the enormous complexity of the total environment, but at least we can explore it at first hand.

The ecological factors in animal distribution were appreciated more than a century ago, for we find Schmarda's division of the earth into regions based in part on considerations that are clearly ecological. In the development of this aspect of biogeography on scientific principles, the botanists took an early lead, and the whole field, for botany, was summarized by A. F. W. Schimper in his important book *Pflanzengeographie auf physiologischer Grundlage* in 1898 (Eng. ed., 1903; 3d German ed. 1935). Thus ecological plant geography was summarized in an authoritative way more than a quarter-century before the appearance of the work by Richard Hesse, *Tiergeographie auf oekologischer Grundlage,* which appeared in 1924. This has now been translated by myself, and quite completely revised by W. C. Allee and myself, for its successive American editions, 1937 and 1951, and it is still by no means as comprehensive a treatment of the ecological aspects of zoogeography as is Schimper's work for phytogeography.

If we search for the roots of ecological animal geography in North America, it is at once evident that they lie in the development of a systematic zoology focused on the existence of subspecies. As long as species were being described from isolated specimens, there might be very little knowledge of their actual geographic ranges; but at the next level of analysis, the very idea of partitioning the species into subspecies required a definition of the ranges of both; and from such knowledge the step was easy to further ecological analysis of the *meaning* of the geographic ranges, and of analysis of the factors limiting such range. A school of description of subspecies grew up in North America hand in hand with the ambitious project of C. Hart Merriam for a biological survey of the continent. This in turn was directed into a broadly zoogeographic aspect by Merriams' development of the life zone theory (1890, 1898), in which the correspondence of altitude zones of mountains with the transcontinental climatic zones was pointed out, with an elaborate explanation of their temperature limitation. Merriam's theory does not bear critical examination, though it was maintained for more than thirty years, and the work of the great United States Biological Survey was set in the Life Zone framework. Fortunately, the question of the existence of life zones is quite independent of the problems of their explanation. Merriam thought that northward distribution is limited by the sum of the positive temperatures (defined as degrees above an assumed physiological zero of 6°C) during the entire season of growth and reproduction, whereas southward limits were set by the mean temperature of a brief period during the hottest part of the year. That this was an extreme oversimplification is now evident; it is necessary to consider maximum and minimum temperatures; average temperature of the coldest part of the year; length and temperature of the frost-less season; amount of rainfall; degrees of atmospheric humidity and wind movement; day length microclimates; the considerable variety of edaphic factors; topographic barriers; and especially the complex of influences introduced by the sum of the favorable and unfavorable biotic factors. A thoroughgoing critique of the theory has been supplied by the botanists Livingston and Shreve (1921) and the zoologists Dice (1923), Kendeigh (1932), Shelford (1932), Daubenmire (1938), and Pitelka (1941), to which list many more names might be added. The idea of temperature summation, originated as an ecological technique by Réaumur in 1735, is by no means to be discarded as useless—it remains as a measure of available heat supply in the growing season, and as one among the many factors that an ecological biogeographer must examine.

Even the summed temperatures finally listed by Merriam have been found to have included an overlooked fundamental error. How could a theory founded on so inadequate and one-sided an explanation of the facts have been so long maintained and served so well as a guide for the exploration of North America? It is simply that the facts of the distribution of plant and animal life in a pattern related to the transverse climatic zones on a continental scale and to the altitude zones in mountains are quite independent of attempted explanations. It can scarcely be too much emphasized that animal life is dependent on plant life in far more ways than a diagram of food relations of plants and animals indicates. Animals live in a plant matrix, whose importance is measured somewhat by the difference in the tropical forest of the order of many thousands to one, and is still very great in the most densely populated savanna. I find this set forth forcefully by Alexander von Humboldt in his *Kosmos* (1845), and as early as 1808 in *Ansichten der Natur*. "Aspects of Nature" is in fact the key to the discrimination of the biotic areas for which we are in search; they prove to be precisely those vegetational areas that are visibly distinguishable in the landscape.

The pattern of life zones, which is so conspicuously transcontinental in the open tundra and coniferous forest of northern North America, becomes more and more obscure in the southern half of the continent, and the Carolinas and California are radically distinct in both vegetation and fauna. The governing factors toward the south become more clearly those of humidity and rainfall instead of temperature, and there is then the further increase in complexity of the historical factors. We may accordingly turn to a much more complicated partition of the continent into biotic provinces. Work in this direction is exemplified in papers by Shelford and Pitelka, and especially by the little book by Lee R. Dice, *The Biotic Provinces of North America* (1943).

Various papers by C. C. Adams deal with problems of animal geography from an ecological standpoint, and with his assistant at the University of Michigan, Alexander G. Ruthven (subsequently director of the University Museum), he focused interest on ecology in museum field work. His paper on the dispersal of the biota of the southeastern United States (1903) well illustrates these interests. Through Ruthven he left a permanent stamp on the Museum of Zoology of the University of Michigan, and Ruthven's lectures on zoogeography influenced a generation of students.

Distributions of the past were of course quite as much determined by the total ecology as those of the present; but we can only discern those paleoecological factors with difficulty and with much more critical attention to the modes of occurrence of fossils than has been thought necessary hitherto. This is, however, a fully recognized direction of effort in geology, and we have in progress a cooperative *Treatise on Marine Paleoecology* of monumental proportions. Paleoclimatology, more specifically of the land areas, has had long attention, and is summarized in special works such as Brooks' *Climate Through the Ages* (2d ed. 1949).

Two papers may be cited as exemplars of paleoclimatology applied to zoogeographic studies. The first of these is Alfred Nehring's classic *Ueber Tundren und Steppen der Jetzt- und Vorzeit* (1890). Nehring analyzes the fauna of the existing northern tundra and of the existing Asiatic steppes (the semi-arid grasslands), and then examines fossil finds of these tundra and steppe animals in Europe in relation to the advances and retreats of the continental glaciers of the

Pleistocene. In certain places there is a succession of deposits in which the life of the tundra (lemmings, reindeer, arctic fox) is found to be replaced by animals characteristic of the open steppe (such as lion, hyena, hamster, and jerboa), and this in turn by the remains of the aurochs and the modern fauna. He interprets this as reflecting the succession of climates and of vegetations associated with the retreat of the ice. In one of my own papers, I have been able to demonstrate a close parallel to the European westward extension of the steppes of Central Asia, in the eastward range of a part of our North American Great Plains fauna in the so-called "Prairie Peninsula" between the Great Lakes and the Ohio (Schmidt, 1937).

Paleoclimatology in relation to the Pleistocene glaciations rests on abundant and conclusive evidence, with the extraordinary advantage in recent years of more exact dating by Carbon–14 analysis. As applied by Brooks and others to ancient climates, with different configurations of the continents, it has the same extremely speculative nature as the paleogeography on which it depends.

At the very root of the problem of geographic range of the species we come upon the problems connected with the range of the individual animal, and more especially of the individual mated pair of breeding aggregations. Illuminating observations have been made on the establishment of well-defined territories in relation to their nests and to their feeding ground by birds, and these are being extended by critical observations to other groups of animals of the most diverse type. We are fortunate to have a summary of this important field of study by Mrs. Margaret Morse Nice "The Role of Territory in Bird Life" (1941), which includes a sketch of the history of the idea. The phenomenon is made conspicuous among birds by the songs of the males, which seem to be effective in establishing their spaced territories. The phenomenon in other animals may be complicated by the degree of social organization; the subject is summarized in *The Principles of Animal Ecology* (Allee *et al.,* 1949).

Island Life

The problem of accounting for the life on islands in the sea has been close to the heart of animal geography from the earliest beginnings of thought. It became a crucial problem to Darwin in relation to giving up the doctrine of special creation in favor of a long-continued natural process. He at once set about making experiments on the viability of seeds after immersion in sea water; and began to assemble the observations of accidental transport of small animals by large, and of animals in general by floating vegetation, which he reports in the *Origin of Species.* Dispersal and capacity for dispersal are, in fact, basic to the whole of animal and plant geography. It is the denial of any capacity for transoceanic dispersal that lies at the root of the whole bridge-building controversy, and in part at the root of the arguments for continental drift. So convinced are the "connectionists" that there can be no overseas transport of land animals that the Galapagos Islands and the Hawaiian Islands have been thought to be quite as necessarily linked to the nearest continent as Britain and Borneo. It is one of the principal accomplishments in animal geography in recent decades to make a renewed analysis of such island life with the conclusion that the islands are indeed oceanic, and that the very existence of their land fauna proves its capacity for overseas dispersal. The most notable advance in our understanding of such distributions has come with the appreciation of the importance of aerial dispersal by winds. The fact, for example, that the Hawaiian spider fauna consists exclusively of those families that disperse by means of gossamer flights is essentially conclusive as to their wind-blown origin. The complete renewed analysis of the Hawaiian fauna by Elwood C. Zimmerman confirms the disharmonic nature of that fauna already evident in the earlier *Fauna Hawaiiensis* of R. C. L. Perkins. In his introductory volume for *Insects of Hawaii* (1948) Zimmerman presents a masterly and conclusive review of the problem of origin of the fauna. He finds it to be undoubtedly the growth of ages of flotsam-jetsam overseas immigration combined with wind-blown insects and accidental arrivals of strayed and off-course land birds.

The West Indies have been a classical meeting ground for speculations as to the origin of their fauna and as to possible land connections with Central and South America. The much more radical idea that they had been directly connected by land with the Mediterranean region, via North Africa, as in Joleaud's *Hipparion* bridge, crops up repeatedly. This is adopted by Jeannel to account for the presence of certain carabid beetles in the West Indies, namely of species whose congeners are found in the Atlantic Islands and North Africa or in the Old World generally. P. J. Darlington, Jr. (1938) has brought this problem into focus as a problem of dispersal; pointing out that the beetles cited by Jeannel as indicating land connection are among the smallest members of the carabid beetle fauna of the West Indies, which enormously increases the probability of their aerial dispersal. When the prevailing winds are plotted, and hurricanes and their tracks considered, the probabilities of arrival of these isolated elements of the West Indian fauna by aerial dispersal become overwhelmingly great.

Darlington's discussion of aerial dispersal of insects is a return to Darwinian thinking about the problem of dispersal in general. A notable contribution to the problem of the possibilties and probabilities of aerial dispersal is supplied by direct studies of the objects found in the air by airplanes. The paper by P. A. Glick, "The Distribution of Insects, Spiders, and Mites in the Air," published in 1939, summarizes data on collections made by means of special traps placed on airplane wings. More than 30,000 specimens of eighteen orders of insects, plus the spiders and mites, were obtained at altitudes ranging from 200 to 15,000 feet, the highest altitude being represented by a single specimen of spider. These observations establish beyond doubt the possibility of dispersal of small creatures of all kinds through the air. The most recent summary of the data of this kind is by Gislén, in 1948.

Life of Fresh Waters

Aerial dispersal had long before been shown to be the explanation of the strikingly wide distributions of freshwater organisms. Bodies of fresh water are usually sharply isolated, and by analogy with isolation on land, their life might be expected to exhibit great corresponding differences from lake to lake and from river to river, which is not found to be the case. The English geologist Thomas Belt further amplified the simple explanation of the wide uniformity of freshwater life offered by Darwin. He was much impressed, in Nicaragua, as

Darwin had been in Brazil, by the radical difference in every aspect of land life from that familiar to him in England, and was the more astonished at the obvious similarities between the freshwater animals of tropical America and those of his native country. In *The Naturalist in Nicaragua,* published in 1874, he points out the fact that bodies of fresh water are in general relatively short-lived, at least in any geologic sense. This, on one hand, snuffs out the variations that develop, while on the other, it puts a premium on the capacity for dispersal. Many kinds of the smaller aquatic organisms have resting stages in which they may dry out and become a part of the dust blown up from a dried lake bottom or river bed. The great uniformity of the smaller animals of the fresh waters of North America and Europe is noteworthy even in the North American Great Lakes, which are no older than the last great advance of the continental glaciers.

The effects of really long continued isolation in older bodies of water are thus all the more impressive and instructive, with many remarkable side lights on species formation. Lake Baikal in eastern Siberia, the Caspian Sea, Lake Tanganyika, and a very few others are preglacial in age, some perhaps dating from the mid-Tertiary; in each of these, animal life has evolved under strict isolation into wonderful series of endemic forms. We are fortunate to have a review of this subject by John Langdon Brooks (1950). To a somewhat lesser extent, the great river systems, like the Mississippi, the Danube, and the Yangtze are also ancient and isolated fresh waters, with strikingly peculiar animal types confined to them. The remnants of former lakes and river systems in old continental arid regions preserve an especially interesting record of origin and of subsequent isolation of their faunas. The phenomena of speciation in the fishes of the desert basins of the western United States have been summarized by Hubbs and Miller (1948).

Another important advance in the study of the problems of dispersal has been made by analyzing the capacity for adjustment to brackish and salt water by freshwater fishes. It is evident that this capacity is much greater than has been suspected; and it is evident also that the limitation of the distribution of freshwater fishes by salt water barriers is a phylogenetic phenomenon; Myers (1949) formulated these ideas by grouping freshwater fishes according to their capacity for dispersal. His groups are: Primary, strictly intolerant of salt water; Secondary, rather strictly confined to fresh water, but relatively salt tolerant, at least for short periods; Vicarious, presumably nondiadromous freshwater representatives of primarily marine groups; Complementary, freshwater forms of marine groups, often diadromous, which become dominant in fresh water only when the first three divisions are absent; Diadromous fishes that migrate from fresh to salt water and vice versa; and Sporadic, for fishes that live and breed indifferently in salt or fresh water, without a fixed pattern of migration.

Isolation and Speciation

An ecological and evolutionary field of study that has been emphasized since the time of Darwin relates to the first beginnings of the origin of species. Darwin apparently greatly underestimated the role of geographic isolation in the separation of an incipient species from its parent form or from related forms, and this was first adequately emphasized by Moriz Wagner, the traveler and collector, whose attention was called to changes *at the species level* from one area to another when a discernible barrier intervened. Wagner's papers on the topic (1868–1886) were collected by his nephew and published in 1889 under the title *Die Entstehung der Arten durch räumliche Sonderung.* The importance of this aspect of animal geography is underlined in recent work in genetics and its relation to systematic botany, zoology, and paleontology. I need mention only Julian Huxley's *The New Systematics,* 1940, Ernst Mayr's comprehensive *Systematics and the Origin of Species,* 1942, and Allee, *et al., The Principles of Animal Ecology,* 1949. The phenomena of speciation are of especial interest in older bodies of fresh water and on older oceanic islands as may be seen in Brooks' and Zimmerman's papers cited above.

Animal Geography of the Sea

The vast and distinct field represented by the animal geography of the sea is in many respects extremely different from that of the land. Partition into faunal regions and provinces goes back to Schmarda (1853) and was thoughtfully reviewed by Ortmann in 1896. Barriers are much less likely to be physiographic, are more likely to be related directly to temperature, and when physiographic, may also depend on mere distance. In one important respect, marine zoogeography is complementary to terrestrial zoogeography, namely in the analysis of the phenomenon of interruption of a land connection by the sea, when the new sea passage becomes a highway for dispersal of marine forms as soon as the land highway is broken. The separation of the continents of North and South America during the Tertiary involves a union in this area of the Atlantic and Pacific. The faunal relations thus produced were long ago pointed out by Jordan (1908); they are adequately summarized by Sven Ekman in his *Tiergeographie des Meeres* (1935), of which a revised edition in English has recently appeared. Ekman sketches a most convincing picture of the major features of the world pattern of distribution of marine forms, of the operation of the open eastern Pacific and of the Atlantic as barriers to the coastal faunas, and of the historic importance of the Tethys Sea.

Conclusion

Animal geography is essentially an evolutionary study. It is only with difficulty definable as a separate science. In its descriptive branch it is one of the aspects of general natural history. If the contents of the eleven volumes on vertebrates of Brehm's *Tierleben* were rearranged by geographic areas, we should have a comprehensive descriptive animal geography in eleven volumes. Interpretive zoogeography is so intimately related to ecology that it must always be considered as a branch of that synthetic science. Historical zoogeography, finally, is directly dependent on paleontology and thus in turn on geology. These intimate relations with several distinct sciences form the great merit of and the abundant justification for a science of animal geography. We have now long realized that specialization must be balanced by synthetic sciences that bridge the gaps between the specialties and break down the barriers between the scientists. It is good to turn from small to large problems, to take the long view, to think sometimes in terms of the world as a whole. Only then can we appreciate and interpret our own geography. And only thus may we attain the unstated but implicit goal of biological studies—an understanding of "Man's Place in Nature."

BIBLIOGRAPHY

ADAMS, CHARLES C.

1903. Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull., 3:115–131.

AIRY, GEORGE BIDDELL

1856. An account of the pendulum experiments undertaken in the Harton Colliery for the purpose of determining the mean density of the earth. Philos. Trans. Roy. Soc. London, 1856:297–356.

ALLEE, W. C., ALFRED E. EMERSON, ORLANDO PARK, THOMAS PARK, and KARL P. SCHMIDT

1949. Principles of Animal Ecology. xii + 837 pp., 263 figs. Philadelphia: Saunders.

ARLDT, THEODOR

1907. Die Entwicklung der Kontinente und ihrer Lebewelt, ein Beitrag zur vergleichenden Erdgeschichte. xxx + 729 pp., 17 text figs., 23 maps. (2nd ed., 1936, 1938.) Leipzig: Engelmann.

1919–1922. Handbuch der Palaeogeographie. 2 vols., illus. 1647 pp., 100 text figs. Leipzig: Borntraeger.

BAKER, H. B.

1912. The origin of continental forms, II. Ann. Rept. Mich. Acad. Sci., 1912:116–141.

BELT, THOMAS

1874. The Naturalist in Nicaragua: a Narrative of a Residence at the Gold Mines of Chontales; Journeys in the Savannahs and Forests with Observations on Animals and Plants in reference to the Theory of Evolution of Living Forms. xvi + 403 pp., illus. London: Murray.

BROOKS, C. E. P.

1949. Climate through the Ages: a Study of the Climatic Factors and Their Variations. Rev. ed. 395 pp., 39 figs. New York: McGraw-Hill.

BROOKS, J. L.

1950. Speciation in ancient lakes. Quart. Rev. Biol., 25:30–60, 131–176, 8 figs.

CAMP, W. H.

1947. Distribution patterns in modern plants and the problems of ancient dispersals. Ecol. Monogr., 17:159–183, figs. 1–32.

CHAMBERLIN, T. C., and R. D. SALISBURY

1904–1906. Geology. 3 vols., illus. New York: Holt.

CHANEY, RALPH W.

1947. Tertiary centers and migration routes. Ecol. Monogr., 17:139–148.

COLBERT, EDWIN H.

1952. The Mesozoic Tetrapods of South America. Bull. Amer. Mus. Nat. Hist., 99: 237–254, figs. 27–28.

DANA, JAMES D.

1880. Manual of Geology: Treating of the Principles of the Science with Special Reference to American Geological History. 3rd ed. (1st ed. 1863). xiv + 911 pp., 12 pls., 1,159 text figs. (P. 797). New York: Ivison, Blakeman, Taylor.

DARLINGTON, P. J., JR.

1938. The origin of the fauna of the greater Antilles, with discussion of dispersal of animals over water and through the air. Quart. Rev. Biol., 13:274–300, 5 figs.

DARLINGTON, P. J. JR. (Cont.)

1948. The geographical distribution of cold-blooded vertebrates. Quart. Rev. Biol., 23:1–26, 105–123, 5 figs.

DARWIN, CHARLES R.

1859. Geographical distribution. Chapts. 12 and 13 *in* The Origin of Species. ix + 502 pp. London: Murray.

DAUBENMIRE, REXFORD F.

1938. Merriam's life zones of North America. Quart. Rev. Biol., 13:327–332.

DICE, L. R.

1923. Life zones and mammalian distribution. Journ. Mammal., 4:39–47.

1943. The biotic provinces of North America. viii + 78 pp., 1 map. Ann Arbor: Univ. Michigan Press.

DU TOIT, ALEXANDER L.

1937. Our Wandering Continents: an Hypothesis of Continental Drifting. xiii + 366 pp., 48 figs. London: Oliver and Boyd.

EKMAN, SVEN

1935. Tiergeographie des Meeres. 542 pp., 244 figs. Leipzig: Akadem. Verlagsges.

FORBES, EDWARD

1846. On the Connexion between the distribution of the existing Fauna and Flora of the British Isles, and the geological changes which have affected their area, especially during the epoch of the Northern Drift. Mem. Geol. Surv. Great Britain, 1:336–432.

FORBES, H. O.

1893. The Chatham Islands, their relation to a former southern continent. Roy. Geogr. Soc. Suppl. Pap. III, pp. 607–637.

GILMORE, C. W.

1943. Fossil lizards of Mongolia. Bull. Amer. Mus. Nat. Hist., 81:361–384, pls. 52, 22 text figs.

GISLÉN, T.

1948. Aerial plankton and its condition of life. Biol. Rev., 23:109–126.

GLICK, P. A.

1939. The distribution of insects, spiders, and mites in the air. U. S. Dept. Agr. Tech. Bull., 673:1–151, 5 pls., 5 text figs.

GÜNTHER, ALBERT

1858. On the geographical distribution of reptiles. Proc. Zool. Soc. London, 1858: 373–398.

HANDLIRSCH, ANTON

1937. Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme. Ann. Naturhist. Mus. Wien, 48:1–140.

HAUG, EMILE

1922. Traité de géologie. 2 vols. (in 3), illus. Paris: Armand Colin.

HEDLEY, CHARLES

1895. Considerations on the surviving refugees in austral lands of ancient antarctic life. Proc. Roy. Soc. New South Wales, 29:278–286.

HEILPRIN, ANGELO

1887. The Geographical and Geological Distribution of Animals. xii + 435 pp., 1 map. New York: Appleton.

Hesse, Richard

1924. Tiergeographie auf oekologischer Grundlage. xii + 613 pp., 135 figs. Jena: Fischer.

Hesse, Richard, W. C. Allee, and Karl P. Schmidt

1937. Ecological Animal Geography. xiv + 597 pp., 135 figs. New York: Wiley.

Hooker, Joseph D.

1853. Flora Novae Zealandiae. Vol. II of The Botany of the Antarctic Voyage of H.M. Discovery-Ships "Erebus" and "Terror" in . . . 1839–1843 under the Command of Captain Sir J. C. Ross. 3 vols. London.

Humboldt, Alexander von

1808. Ansichten der Natur, mit wissenschaftlichen Erläuterungen. viii + 344 pp. Tübingen.

1844. Kosmos. Entwurf einer physischen Weltbeschreibung. 4 vols. Stuttgart: Cotta.

Hutton, F. W.

1873. On the geographical relations of the New Zealand fauna. Trans. New Zealand Inst., 5:227–256.

1896. Theoretical explanations of the distribution of southern faunas. Proc. Linn. Soc. New South Wales, 21:36–47.

Huxley, Julian (ed.)

1940. The New Systematics. viii + 583 pp., illus. Oxford: Oxford Univ. Press.

Huxley, Thomas H.

1868. On the classification and distribution of the Alectoromorphae and Heteromorphae. Proc. Zool. Soc. London, 1868:294–319, figs. 1–16, 1 map.

1870. Anniversary address of the president. Quart. Journ. Geol. Soc. London, 26: xxi-lxiv.

Ihering, Hermann von

1891. On the ancient relations between New Zealand and South America. Trans. New Zealand Inst., 24:441–445. (Transl. from Das Ausland, No. 18, 1891.)

Jeannel, René

1935. L'Archatlantis et le peuplement de la region mediteranéene. Arch. Mus. Hist. Nat. Paris, (6)12:413–426, 6 figs.

1941. Au Seuil de l'Antarctique. . . . Éditions du Museum, No. 5. 236 pp., 16 pls., 27 text figs. Paris.

Joleaud, L.

1924. L'histoire biogéographique de l'Amerique et la théorie de Wegener. Journ. Soc. Amér. Paris, n.s., 16:325–360.

Jordan, D. S.

1908. The law of geminate species. Amer. Nat., 42:73–80.

Kendeigh, S. Charles

1932. A study of Merriam's temperature laws. Wilson Bull., 44:129–143, figs. 27–28.

Marcou, Jules

1860. "Géographie antediluvienne." [Not seen.] *In* Raymond Furon, Le Jura dans les deux hémisphères. Carte globe a l' époque jurassique monstrant la distribution des terres et des mers. Pp. 168–169. 1941.

Matthew, W. D.

1915. Climate and Evolution. Ann. N. Y. Acad. Sci., 24:171–318, 33 figs. Reprinted as Spec. Publ. New York Acad. Sci., 1:xi + 223 pp., 33 figs., 1939.

Mayr, Ernst

1942. Systematics and the Origin of Species. xiv + 334 pp., 29 figs. New York: Columbia Univ. Press.

Merriam, C. Hart

1890. Results of a biological survey of the San Francisco Mountain region and the desert of the Little Colorado, Arizona. North American Fauna, 3:1–136, pls. 1–13, maps 1–5.

1898. Life zones and crop zones of the United States. Bull. U. S. Dept. Agric., 10:7–79.

Myers, George S.

1938. Fresh-water fishes and West Indian zoogeography. Ann. Rept. Smithson. Inst., 1937:339–364.

1949. Fresh-water fishes and East Indian zoogeography. Stanford Ichth. Bull., 4:11–21.

1949a. Salt-tolerance of fresh-water fish groups in relation to zoogeographical problems. Bijdragen tot de Dierkunde, 28:315–322.

Nehring, Alfred

1890. Ueber Tundren und Steppen der Jetzt- und Vorzeit, mit besonderer Berücksichtigung ihrer Fauna. viii + 257 pp., illus. Berlin: Ferd. Dümmlers.

Neumayr, Melchior

1886–1887. Erdgeschichte . . . 2 vols., illus. Leipzig.

Nice, Margaret Morse

1941. The role of territory in bird life. Amer. Midl. Nat., 26:441–487.

Ortmann, A. E.

1896. Grundzüge der marinen Tiergeographie. Anleitung zur Untersuchung der geographischen Verbreitung mariner Tiere, mit besonderer Berücksichtigung der Dekapodenkrebse. iv + 96 pp., 1 map. Jena: Fischer.

1901. The theories of the origin of the Antarctic faunas and floras. Amer. Nat., 35:139–142.

Osborn, H. F.

1900. The geological and faunal relations of Europe and America during the Tertiary Period and the theory of successive invasions of an African fauna. Science, n.s., 11:561–574, 4 charts.

Perkins, R. C. L.

1913. Introduction, being a review of the land-fauna of Hawaii. Fauna Hawaiiensis, 1(pt. 6):xv–ccviii, 16 pls.

Pfeffer, Georg

1905. Die zoogeographischen Beziehungen Südamerikas betrachtet an der Klassen der Reptilien, Amphibien, und Fische. Zool. Jahrb. Suppl., 8:407–442.

Pitelka, Frank A.

1941. Distribution of birds in relation to major biotic communities. Amer. Midl. Nat., 25:113–137, figs. 1–11.

Pratt, J. H.

1855. On the attraction of the Himalaya Mountains and of the elevated regions beyond them upon the plumb line in India. Philos. Trans. Roy. Soc. London, 1855:53–100.

Réaumur, René A. F. de

1735. Observations du thermométre. Mem. Acad. Roy. Sci., Paris, 1735:545–576.

RÜTIMEYER, C. I.

1867. Ueber die Herkunft unserer Thierwelt. Eine zoogeographische Skizze. . . . Mit einem Verzeichniss der fossilen und lebenden Schweizerischen Säugethiere und einer Karte zur Andeutung der Geschichte der Tierverbreitung im Allgemeinen. 57 pp., 1 map. Basel.

SCHARFF, R. F.

1909. On the evolution of continents as illustrated by the geographical distribution of existing animals. Proc. 7th Internat. Zool. Congr., pp. 1–14. Boston.

SCHIMPER, A. F. W.

1898. Pflanzengeographie auf physiologischer Grundlage. xviii + 876 pp., 69 pls., 4 maps. Jena: Fischer.

SCHMARDA, LUDWIG K.

1853. Die geographische Verbreitung der Thiere. viii + 755 pp., 1 map. Wien: C. Gerold and Son.

SCHMIDT, K. P.

1937. Herpetological evidence for the postglacial eastward extension of the steppe in North America. Ecology, 19:396–407, figs. 1–9.

1943. Corollary and commentary for "Climate and Evolution." Amer. Midl. Nat., 30:241–253.

SCLATER, P. L.

1858. On the general geographical distribution of the members of the class Aves. Journ. Linn. Soc., 2(zool.):149–170.

SCRIVENOR, J. B., I. H. BURKILL, MALCOLM A. SMITH, A. STEVEN CORBET, H. K. AIRY SHAW, P. W. RICHARDS, and F. E. ZEUNER.

1943. A discussion of the biogeographic division of the Indo-Australian Archipelago with criticism of the Wallace and Weber lines and of any other dividing lines and with an attempt to obtain uniformity in the names used for the divisions. Proc. Linn. Soc. London, 154 Sess., pp. 120–165, 2 figs.

SHELFORD, VICTOR E.

1932. Life zones, modern ecology, and the failure of temperature summing. Wilson Bull., 44:144–157, figs. 29–34.

SHUCHERT, CHARLES

1932. Gondwana Land Bridges. Bull. Geol. Soc. Amer., 43:875–916, pls. 24, 2 text figs.

SIMPSON, GEORGE GAYLORD

1940. Mammals and land bridges. Journ. Wash. Acad. Sci., 30:137–163, 6 figs.

1943. Turtles and the origin of the fauna of Latin America. Amer. Journ. Sci., 241: 413–429.

1943. Mammals and the nature of continents. Amer. Journ. Sci., 241:1–31.

1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. Amer., 58:613–687, figs. 1–6.

1950. History of the fauna of Latin America. Amer. Sci., 38:361–389, figs., 1–10.

SUESS, EDUARD

1904–1924. The Face of the Earth. (Das Antlitz der Erde.) 5 vols., illus. (1st ed. 1883–1909). Oxford: Clarendon Press.

TAYLOR, F. B.

1910. Bearing of the tertiary mountain belt on the origin of the earth's plan. Bull. Geol. Soc. Amer., 21:179-226.

WAGNER, MORIZ

1889. Die Entstehung der Arten durch räumliche Sonderung. Gesammelte Aufsätze. 667 pp. Basel: Benno Schwabe.

WALLACE, ALFRED RUSSELL

1876. The Geographical Distribution of Animals with a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface. 2 vols., maps, illus. London: Macmillan.

1880: Island Life: or, the Phenomena and Causes of Insular Faunas and Floras, including a Revision and Attempted Solution of the Problem of Geological Climates. xvii + 526 pp., 3 maps, illus. London: Macmillan.

WEGENER, ALFRED

1924. The Origin of Continents and Oceans. xx + 212 pp., 44 figs. London: Methuen.

WILLIS, BAILEY

1932. Isthmian links. Bull. Geol. Soc. Amer., 43:917–952, pls. 25–29.

WITTMANN, OTTO

1934–1935. Die biogeographischen Beziehungen der Südkontinente. Zoogeographica, 2:246–304, 12 figs.; 3:27–65, 10 figs.

ZIMMERMAN, ELWOOD C.

1948. Introduction. (Vol. I). *In* Insects of Hawaii. vii–xvii + 1–206 pp., 52 figs. Honolulu: Univ. Hawaii Press.

THE CONSERVATION OF WILDLIFE

By A. STARKER LEOPOLD
Museum of Vertebrate Zoology, University of California, Berkeley

In the year 1852 the Legislature of the new State of California passed a law protecting deer from hunting for six months of the year. This event marked the beginning of wildlife conservation in the West.

In the year 1952 several branches of the California state government spent $3,379,000 on fish and game management (Calif. Dept. Fish and Game, 1953) and the state legislature had on its docket over 150 bills affecting wildlife in one way or another. During the intervening century there had evolved a complicated set of concepts and administrative programs concerned solely with ways and means of preserving and managing wild animal populations. Although the evolution of ideas in wildlife management is proceeding faster now than ever before, it may be well at this point to review the events of the past century as a guide to our future thinking and planning.

Early Beginnings

On the frontier, of course, there was little thought of wildlife preservation. Many a post mortem has been written about the careless treatment of animal resources by our pioneer forefathers. The slaughter of the bison and passenger pigeon, the ruthless commercialization of fur animals, the feather trade, have all been thoroughly lamented and there is no point in retracing the dark and bloody history here. In point of fact, human behavior is so completely conditioned by circumstances as to suggest that our most ardent conservationists today (the author included), had they been born into frontier society, would perhaps have acted much like their contemporaries. The concept of saving something only assumes meaning when that thing becomes scarce. The conservation idea could not have been born until the native wealth of wildlife was clearly being dissipated. Our history of the conservation movement begins, therefore, with the first flickerings of recognition for its need.

From 1852, when the first game-protective law was passed in California, until after 1900, despair over the steady shrinkage of game and fur resources in the West deepened into the conviction that game was ultimately doomed. More and more protective laws were dutifully adopted by the various state legislatures but there is no evidence of real optimism that the laws would stem the receding tide. Since no provision was made for enforcing the game laws, they were largely ignored by the hunting public, a fact well known to the legislators. The passage of game laws was in that era no more than an expression of pious regret that the deer, elk, beavers, and so forth, were yielding to the inevitable advance of settlement. At the most it was hoped that legal protection might serve to ration out the remaining stocks of game—to make the supply last a little longer.

Then at the turn of the century there emerged a President with a firm conviction that permanent preservation of wildlife and of sport hunting could be achieved as part of a general program of resource management. Theodore Roosevelt catalyzed an astonishing advance in conservation thinking. His long association with Gifford Pinchot and other foresters convinced him that wild crops such as forests and game could yield an annual harvest indefinitely if the rate of harvest were properly regulated and a basic breeding stock (or growing stock) were retained. Installed in the presidency in 1901, he determined to make conservation his personal crusade. In the first years of his term, Roosevelt brought public attention to focus on the need for a broad national conservation program and he fanned to life the hope that such a program actually could save some of the native beauty of the countryside. Scientists who had been busy cataloguing and describing the native animals suddenly came forth with a rash of pamphlets and magazine articles on preserving our vanishing wildlife. Newspapers devoted editorials and front page space to this new crusade. State legislatures from coast to coast busied themselves creating new conservation bureaus and departments. As a culmination, in 1908 Roosevelt invited all the Governors of the United States to a White House conference on conservation, and that event gave added stimulus to the movement which already was well under way.

The initial idea of the conservation movement was to *protect* and *preserve* the remnants of wildlife that had not been dissipated by the frontiersmen. Administrative programs were developed to implement various phases of the protective movement, and for the ensuing thirty years wildlife conservation implied in large part simple protection. The concept of managing and producing game crops formulated slowly during this period.

The three principal aspects of protection were (1) legal protection and law enforcement, (2) establishment of refuges and wildlife preserves, and (3) control of natural predators.

Legal Protection

As stated above, game protective laws had little significance until wardens were sent into the field to enforce them. Most state warden forces were organized in the Rooseveltian era, at which time the hunting license was widely adopted as a device for financing law enforcement. Whereas many game-protective laws had been passed in the period from 1677, when Connecticut enacted the first such regulation, until 1852, when the custom reached California, and thousands more were adopted in the late nineteenth century, it was actually in the decade 1900–1910 that effective legal protection was achieved. By then the near-extermination of some of the most numerous of native game species pointed up the great need for hunting control. Enthusiasm for game protection was stirred by the eloquent writings of such leaders as William T. Hornaday (1913, 1914), William Dutcher, Theodore S. Palmer, T. Gilbert Pearson, and John Phillips, and there quickly developed a strong public sympathy for the cause of protection, which of course was essential to its success.

Almost from the start the protection movement brought demonstrable results in the way of game increases. Certain species such as deer and elk, which had been dangerously reduced, responded magnificently when the kill was limited, and this encouraged the conservationists in the firm conviction that they were on the right track. The fact that species whose habitats had been largely destroyed by agriculture and grazing did not respond equally (i.e., bison, pronghorn antelope, bighorn, waterfowl), was generally interpreted as a sign that protection was still inadequate. Efforts were redoubled to supply additional safeguards to these diminishing stocks.

Over the years the structure of legal game protection became more complex. Relatively simple laws were locally modified and refined, and license fees were raised to support constantly expanding warden forces. As an example of this evolution, table 1 traces the changes in seasons, bag limits, and special limitations on the hunting of deer in California. Although the table greatly simplifies legal details, it serves to show the growth of the protection program for a given species in one state.

Table 1. A Chronological Summary of California Deer Hunting Regulations From 1852 to 1950
(*from Longhurst, et al.*, 1952)

Year	*General seasons*	*Bag limit (Bucks)*	*Hunting license*	*Deer tags*	*Remarks*
1852–82	—	—	—	—	Deer protected 6 months of year
1883–92	—	—	—	—	Antlerless deer protected
1893–94	Sept. 1–Oct. 15	—	—	—	
1895–1900	July 15–Oct. 15	—	—	—	
1901–02	Aug. 1–Sept. 30	3	—	—	Night hunting and sale of meat prohibited
1903–04	July 15–Oct. 31	3	—	—	
1905–06	Aug. 1–Oct. 15	2	—	—	
1907–10	July 15–Sept. 30	2	$1.00	—	
1911–14	July 1–Oct. 31	2	1.00	—	6 game districts established
1915–18	Aug. 1–Oct. 14	2	1.00	—	4 game districts
1919–20	Aug. 1–Oct. 14	2	1.00	—	6 game districts; spike bucks protected
1921–24	Aug. 1–Oct. 15	2	1.00	—	Forked-horn bucks protected in northeastern district
1927–45	Aug. 1–Oct. 15	2, most of state; 1 in part	2.00	$1.00	
1946	Aug. 7–Oct. 21	2, most of state; 1 in part	2.00	1.00	
1947	Aug. 7–Oct. 15	2, most of state; 1 in part	2.00	1.00	22 game districts
1948	Aug. 7–Oct. 15	1, most of state; 2 in part	3.00	1.00	
1949–50	Aug. 7–Oct. 15	1, most of state; 2 in part	3.00	1.00	Special seasons on antlerless deer in 3 localities

By the late 1930's and early 1940's, game regulations were becoming so complex as to occupy an undue amount of time and attention on the agendas of state legislatures. In many states, plenary powers were transferred from general legislative bodies to fish and game commissions, which were much better able to cope with the details of regulating the game kill. Today most state laws dealing with wildlife are enacted by special commissions, but legislatures continue to dabble in the field, which still has strong political significance. The effort to remove wildlife administration and regulation from partisan politics has been only partly successful.

Whereas the legal custodianship of most wildlife was vested in the individual states almost from the start of our national history, migratory birds became wards of the United States Government following ratification of a treaty with Canada in 1916 which established the international aspects of the problem. A similar treaty with Mexico was signed in 1937. Thus the federal government assumed an important responsibility in the legal protection of one class of game, and current regulations for the hunting of waterfowl and such other migratory birds as are still taken legally are set each year by the Secretary of Interior upon recommendation of the Director of the Fish and Wildlife Service.

The complicated legal machinery, state and federal, that has been created to protect wildlife from overshooting has come to be considered in the public mind as the skeleton and backbone of wildlife conservation. Though it will always be a necessary part of management, protection has probably been overrated in importance, and now more recognition is being given to habitat management as the principal key to game abundance. This changing point of view will be discussed in a later section.

Refuges and Sanctuaries

At the same time that general protection was extended to American wildlife in the form of legal restrictions on the kill, certain local areas were singled out for more intensive development as sanctuaries. The first of these was Lake Merritt in the City of Oakland, which was designated as a waterfowl sanctuary in 1870 by the California legislature. Subsequently nearly all of the states created numerous refuges embracing millions of acres, the assumption being that on these selected areas, game could flourish and spread out to surrounding lands.

On federal lands, wildlife was given complete protection on the national parks, although not in the first years of their existence. As early as 1864 the United States Congress set aside the Yosemite as a nature reserve but the main objective was to conserve the forest and scenery, not the wildlife. Finally, however, in 1890 the Yosemite, General Grant, Sequoia, and Yellowstone areas, were formerly designated as national parks and in 1894 these areas were closed to hunting, as have been all the national parks and monuments ever since. Many state and municipal parks likewise are maintained as sanctuaries—a good policy in general, for animals that are both abundant and tame may be seen and enjoyed by visitors.

Starting in 1903 the Federal government began withdrawing additional lands as wildlife refuges under the Bureau of Biological Survey, now the Fish and Wildlife Service. Today there are 282 Federal wildlife refuges encompassing 18,500,000 acres (Day, 1949). One hundred and ninety-six of these areas are primarily maintained for migratory waterfowl; the balance, including some of the largest of the Federal refuges, serve to protect various species of upland game and colonial nesting birds.

Supplementing the governmental refuges are many sanctuaries and preserves operated by municipalities, by conservation organizations such as the National Audubon Society, and by individual landowners.

The refuge movement gained momentum during the early years of the protective phase of game management and it reached a peak in the 1920's and 1930's. But as time went on it became clear that refuges *per se* were not the answer to the shortage of huntable game. For migratory waterfowl and for certain rare species of local occurrence the refuge is still and always will be a primary tool of management, but for upland game generally, closing some areas to hunting does not increase the level of game abundance in surrounding terrain. Most nonmigratory species are much too sedentary to "overflow" from a refuge and repopulate the rest of the countryside as had been postulated. Rather, the result of excluding hunters from parts of the game refuge serves merely to concentrate them in nonrefuge lands, thereby decreasing the availability of game to the individual shooter. So the popularity of the refuge waned, and today most states are liquidating their refuge systems for upland game, though retaining those for waterfowl.

Predator Control

The third phase of the game protection program involved removal of predatory animals that were looked upon as "wicked citizens" of the wild community, destroying the breeding stocks that conservationists were striving to restore. Also, these same predators often preyed upon domestic livestock, rendering them doubly wicked in the public eye. And so the wolf and mountain lion, the coyote and bobcat, and many smaller offenders as well, came in for severe treatment.

In addition to normal persecution by farmers, stockmen, and sportsmen, the predators were controlled systematically by special hunters, employed by the states and by the Federal government. Their demise was hastened in many localities by the payment of bounties or subsidies for scalps.

Predator control proved generally to be the least satisfactory protective measure taken in behalf of game.

Some of the large ungulates like deer and elk responded well enough to all this attention, but within fifty years they became so numerous in countless areas as to endanger their own forage supplies. Rigid hunting laws precluded effective control of populations by sportsmen, and removal of large predators such as wolves and lions had taken away the natural controls. In short, overenthusiasm for protecting game when it was scarce led ultimately to even more difficult problems that arose from an excess of game. The first great loss of deer by starvation came on the Kaibab National Forest in Arizona, where a herd of a few thousand was built up to 100,000 in 1924 by rigid protection from hunting and predators. A plea by the Forest Service for reduction of the herd, to save the range, was vigorously denied by state authorities, and in 1925 most of the deer died of starvation. The herd continued to shrink until by 1939 there were only 10,000 left and the range was ruined. That sequence has been repeated a thousand times on deer ranges all over the West, the Lake States, and the Northeast. Today many biologists argue in favor of *less* predator control on big game ranges as a safeguard against population irruptions.

On the other hand, predator control as a measure to increase small game such as quail, pheasants, and rabbits, has never been proved to have any material effect at all. Great sums that have been paid for reduction of foxes, weasels, hawks, owls, and crows, probably have not raised the level of farm game above what the terrain would support anyway.

Like many another sovereign remedy for game shortage, the control of predators did not prove to be a panacea.

Artificial Propagation—the Game Farm Mania

After the program of wildlife protection was well under way, a new approach was devised to give hunters more game to shoot. Various birds and mammals, some native but many exotic, were propagated in pens and liberated in the depleted coverts.

The one great success of the restocking program was the introduction of the ring-necked pheasant from China into farmlands of the northern and central United States. Unfortunately, this initial *coup de maître* inspired great confidence in propagation as a method of increasing game, leading over the years to expensive and usually fruitless attempts to repeat the process with other species. Most of the exotic pheasants, partridges, and grouse that were introduced failed to survive and the few that became established, such as the Chukar and Hungarian partridges, did so on a relatively small scale.

Among native species, repeated studies have shown that pen-raised birds and mammals have a low survival rate and serve scarcely to augment the natural crop of birds, raised in the wild at no expense. Where native stocks were literally exterminated by overhunting or trapping, introducing live-trapped animals from elsewhere often has been successful. For example, elk, antelope, and beaver have reoccupied great areas of range following reintroduction. But it was demonstrated that propagated stocks, for instance, of the wild turkey and the bobwhite quail were sometimes genetically inferior to native stocks in their ability to survive in the wild, and that mixing of the strains actually led to a *decrease* in wild populations. It has been proved that, where a breeding stock of game already exists, there is little advantage in attempting to build it up by artificial propagation.

Habitat Management

The shortcomings of simple protection and of propagation as methods of managing wildlife led finally to appreciation of the habitat as the transcendent force that, more than any other, determines the level of wild populations. It had long been recognized that each wild species was associated with a given sort of habitat and required certain types of food and of cover, but the idea of producing game by the simple expedient of creating a suitable home for it was adopted slowly in this country.

In the Old World, the purposeful preparation of the habitat for game had long since become standard practice. As early as the thirteenth century, Marco Polo noted that Kublai Khan maintained special preserves for partridges and pheasants, ". . . for whose food the Great Khan caused millet, and other grains suitable to such birds, to be sown . . . every season, and gives strict command that no person shall dare to reap the seed; in order that the birds may not be in want of nourishment." The Khan likewise prepared special winter shelters and maintained a staff of gamekeepers to protect both the birds and their habitat. Marco Polo concludes: "In consequence of these attentions, he [the Khan] always finds abundant sport when he visits this country" [near Changanoor, Cathay].

At a somewhat later date in Europe, the planting of special coverts for pheasants and gray partridges became customary on country estates and on crown forests, and in Scotland the rotational burning of heather was found to be the least expensive and most effective way to increase numbers of red grouse.

But these ideas were not carried to the New World. Much was said and written about preserving existing wildlife habitat, as for example on the national forests, but cultural operations to create new or better habitat were not attempted until Herbert Stoddard, then with the United States Biological Survey, undertook to study means of improving bobwhite shooting in Florida and Georgia. Stoddard's work on quail management in the Southeast was a milestone in American conservation. His book on *The Bobwhite Quail* (1931) summarized five years of intensive, scientific study of the bird in its natural environment and pointed up the fact that the management of the land and its vegetation had more to do with quail abundance than hunting, predators, or any other single factor. He showed how simple cultural operations could be used to create food and cover in proper interspersion, yielding a high density of quail and a high annual bag for hunters. Though the book is over twenty years old it is still the bible of game managers on Southern plantations. More importantly, it demonstrated the scientific approach to game production through good land management.

At about the same time, another pioneer in the new era of wildlife management, Aldo Leopold, came forth with two volumes that reiterated Stoddard's findings and applied the basic tenets to game populations generally. The first of these, entitled *Report on a Game Survey of the North Central States* (1931) dealt with game conditions in one specific region. The second *Game Management* (1933), laid down the principles of scientific game production and harvest. From that time on, the study and the administration of wildlife resources was led gradually from the fields of politics and law into the fields of science and land management.

The New Deal of the 1930's was a fruitful period in which scientific game management could grow. The federal government heavily subsidized conservation projects of many kinds, and developing wildlife habitat became a recognized activity of such bureaus as the Soil Conservation Service, Forest Service, Tennessee Valley Authority, and Bureau of Land Management, as well as the Fish and Wildlife Service. State fish and game departments likewise began spending money on game-range improvement instead of limiting their budgets to wardens, hatcheries, and game farms.

The literature of the past decade has reflected this change in viewpoint. Among the important recent additions to the wildlife library are books by Graham (1944, 1947), Trippensee (1948), Grange (1949), and Wing (1951), all of which emphasize the management and conservation of land and vegetation as the basis for game production.

Perhaps of more fundamental importance than the administrative and literary recognition of a scientific basis for game management has been the development of a body of trained professional men in the field. In 1937 a professional society was formed, called The Wildlife Society, which began issuing a technical quarterly, *The Journal of Wildlife Management.* Many universities added trained wildlife men to their staffs, who in turn produced other trained men to fill administrative as well as academic positions. Wildlife management quickly assumed stature as a technical profession, comparable to forestry or the agricultural sciences.

Wildlife Research

Up to the time of Herbert Stoddard there was a decided separation between the scientific study of natural history and the administrative field of wildlife conservation. After Stoddard's demonstration of how scientific study could guide and orient conservation effort, wildlife research mushroomed into a thriving field of activity.

Some of the basic questions which have occupied wildlife students in the past and will continue to keep them busy for years into the future are:

1. Precisely what factors determine or limit wild populations?
2. How do various cultural operations of land, forestry, agriculture, grazing, etc.) affect game populations?
3. By what practicable means can game populations be increased?
4. What yields can and should be taken by hunters?

These seemingly simple queries have proven to be very complex indeed. A digest of the considerable volume of data accumulated to date permits the following tentative summary of the field of population dynamics which underlies the whole theory of management.

Each wild population requires for its existence a number of indispensable components of habitat. These may be categorized under the headings (a) food, (b) cover, (c) water, and (d) special factors, such as grit, dusting facilities, salt, etc. If all of these are present in adequate amounts and in favorable juxtaposition a population may exist. If the habitat is favorable, the density of the population will be high. But if one or more of the environmental factors is limited in amount or in availability the population will tend to be less dense. The average level of a game population is therefore a function of the "carrying capacity" of the local habitat, a term used to express the sum effect of the environment on the population. Thus, one area may support 50 deer per square mile but a similar tract with less forage might support only 30 deer per square mile. Food supply in the latter area is the factor limiting the population. Or, one quail population might be lower than another because cover or perhaps water was inadequate, hence limiting.

Whatever the level of a local game population, it reproduces annually and creates a "surplus," which in one way or another will be dispersed prior to the next breeding season. The surplus may be shot by hunters, or it may be taken by predators, or disease, or accidents. The important thing is that it will disappear. The annual increase in wild populations, which may be as low as 10 per cent in bears or as high as 300 per cent in quail, is never saved in a fully stocked habitat, but tends to be vulnerable to many kinds of losses, down to the level of "carrying capacity." Below that level, losses are few. These principles were first stated by Errington (1934, 1936, 1943) based on studies of bobwhites in Wisconsin and muskrats in Iowa. They have been verified by many subsequent investigations of other species in a variety of habitats and give support to the idea that management should strive to raise the carrying capacities of local environments as the cheapest and surest way to increase game.

But these general concepts served merely to orient thinking without defining the specific nature of the relationships between vertebrate organisms and their environments. Recent research has sought to refine our understanding of "carrying capacity" and of the reaction of individual animals to their surroundings and to each other.

Considerable attention has been focused, for example, on the question of game nutrition. Even a few years ago, anything a bird or mammal ate was considered "food" and the only measure of importance applied to items of diet was quantitative. But it was noted that some types of food supported higher populations than others, and this led to investigations in qualitative nutrition. Among the various sorts of winter browse eaten by deer, for example, those species that seem best to maintain the animals have proved to be high in protein. On an adequate protein diet, deer remain strong and vigorous through the winter, the does bear many healthy fawns, and young adults breed at an early age. Conversely, on low protein the deer weaken, become subject to high losses from predators, disease, or outright starvation, and they raise few fawns (Longhurst *et al.*, 1952). Thus food quality has a great deal to do with carrying capacity of deer ranges by regulating both the rate of increase and the extent of loss in the herds. Parallel studies of production and loss in quail populations suggest that there may be similar striking effects of changing quality in the diet.

Another phase of ecology that is being much studied today is the matter of competition between members of a population and how competition serves to regulate population levels. Besides competing for food and for the best areas of cover, members of a dense population seem to affect each other in some subtle way that lowers reproductive rate. Thus in populations of bobwhite quail, ring-necked pheasant, mule deer, and brown rats, the rate of fecundity per individual female has been found to be inversely proportional to the density of the population. The most precise measure of this phenomenon has been made in rat populations in the city of Baltimore (Emlen *et al.*, 1948; Davis, 1951). Following artificial reduction of the rats to a low level, there was a marked increase in the size and frequency of litters produced by the surviving females. As the population again approached carrying capacity, fecundity decreased until a stable population was restored, in which death rate and birth rate balanced. The obvious implication in management is that a heavy artificial kill, as by hunting, is compensated by an increased birth rate—a vital point in determining desirable rates of harvest.

These examples serve to indicate the trends in current wildlife research. From this type of work on basic principles of population dynamics will inevitably come a better understanding of the critical or limiting factors that regulate wild populations. Such knowledge in turn will guide future efforts in management.

So rapid has been the progress in wildlife studies of the past decade that administrative procedures have been unable to keep pace with the changing ideas. Thus programs of predator control, artificial propagation, and close regulation of the kill that evolved over the past half-century are not easily abandoned immediately upon discovery that there are better ways to expend available funds. Considerable investments in game farms and personnel trained in certain activities must be amortized and converted slowly to new undertakings. Likewise, public opinion, which strongly influences legislation and administrative proceedings, must be reoriented periodically in line with scientific findings.

Nevertheless, wildlife research in the past twenty years has had a tremendous influence on management policy, and that influence can be expected to grow in the future.

Wildlife and Land Use

American land is being used more and more intensively to feed a nation that still is growing. Agriculture, grazing, forestry, and watershed protection are all primary uses of the land that in most areas will take precedence over wildlife production. If sport hunting is to be maintained as a form of outdoor recreation available to one and all, it will have to be carefully oriented to other forms of land use.

Fortunately, game often may be produced in quantity on lands that are primarily dedicated to other uses. Thus, forest lands devoted to growing timber may, with only slight modification of management, also grow deer. Grain and pasture lands can produce a side crop of quail and pheasants. Meadows and sloughs can yield both beef and ducks. The task of wildlife research is to achieve an understanding of game populations and habitat relationships that will permit such dual planning of land use. The administrative task is to apply this knowledge.

There are many practical difficulties to overcome in maintaining an optimum habitat for game on dual-use lands. Private landholders, for example, operate their farms and ranches primarily to produce marketable crops, and as yet there is no financial motive to spend time and money on habitat improvement for game. But many land practices that are of profit to the landowners also promote game crops. Fencing and planting gullies to prevent erosion creates coverts for wildlife as well. Many range practices that improve brushlands for cattle also benefit deer. Building farm ponds to conserve water for livestock and for irrigation creates habitat for ducks and some fur-bearers. Wildlife management is best sold to landowners then "via the back door"—as a secondary benefit of some profitable aspect of good farming.

This places fish and game administrative bureaus in the position of being promoters of game production on lands not under their control. By subsidies and technical assistance they can induce a certain amount of habitat improvement on private lands. But the key man in the future of American wildlife will continue to be the individual landowner. Recognition of this fact has led to increasing emphasis on conservation education and extension work among farmers and ranchers.

The effective development of wildlife management on private lands is being seriously hindered by the legal machinery set up fifty years ago during the protective phase of game conservation. Ownership and custody of the game has been definitely placed by the courts in the hands of public agencies whose regulations governing hunting are in turn dictated in large part by organized sportsmen, not by the landowners who in fact are the real custodians of the game range. Rigid laws prevent the landowner from marketing a game crop in the way he markets his wheat or lambs, yet he is being asked to produce the crop for the public to harvest. Various legal devices such as cooperatives and licensed shooting preserves are now being tested to circumvent this problem, but with only partial success. Short seasons and unnecessarily conservative hunting laws still serve to discourage game management as a business enterprise on most private lands. In other words, there are traditional, educational, fiscal, and legal barriers to general application of research findings on how to produce game.

On public lands the problem is relatively much simpler. For example, on the national forests game and fish production for public recreation is recognized as an important and in some areas as a primary use of the land. The Forest Service is not impelled solely by financial motives in establishing its land use policies, and where the public good is best served by devoting areas to wildlife (as for example, deer winter ranges, or reserves for rare species), conflicting uses may be excluded or made subservient. Noticeably more progress is being made in adopting scientific methods of game production on public lands than on private.

It is clear, however, that on all lands throughout the nation there has been steady progress in adopting new and more effective methods of encouraging wildlife, and there is every reason to hope that substantial populations of shootable game, and of nongame native forms as well, can be retained despite intensified use of land resources. Recognition of the importance of outdoor recreation in modern society has placed a premium on wildlife which will stimulate added effort among conservationists of the future.

Summary

Wildlife conservation in the United States started as an effort to preserve remnants of the native animal populations that had been severely depleted during the era of frontier exploitation. The initial stages were protective in nature and consisted principally of legal restrictions on hunting, setting aside refuges and sanctuaries, and controlling natural predators.

After the protective program was well developed, a few trained biologists began to study game ecology in the field and learned that maintaining a suitable habitat for game was far more effective in sustaining wild populations than merely protecting existing breeding stocks. There followed a rapid reorientation in conservation thinking and a parallel but slower adjustment in administrative programs.

One outgrowth of the success of the biological approach to wildlife management was the development of a technical profession, with training facilities in universities, accelerated research, and publication of scientific literature on game. In a very short time the nature of the profession changed from a quasi-legal and political undertaking to a scientific field comparable to forestry or the agricultural sciences.

LITERATURE CITED

CALIFORNIA DEPARTMENT OF FISH AND GAME

1953. Forty-second Biennial Report. 187 pp. Sacramento: Calif. State Printing Office.

DAVIS, DAVID E.

1951. A comparison of reproductive potential of two rat populations. Ecology, 32(3): 469–475.

DAY, ALBERT M.

1949. North American Waterfowl. xx + 329 pp. New York: Stackpole and Heck, Inc.

EMLEN, J. T., JR., A. W. STOKES, and C. P. WINSOR

1948. The rate of recovery of decimated populations of brown rats in nature. Ecology, 29(2):133–145.

ERRINGTON, PAUL L.

1934. Vulnerability of bob-white populations to predation. Ecology, 15(2):110–127.

1943. An analysis of mink predation upon muskrats in north-central United States. Iowa State Coll. Agri. Res. Bull. 320, pp. 797–924.

ERRINGTON, PAUL L., and F. N. HAMERSTROM, JR.

1936. The northern bob-white's winter territory. Iowa State Coll. Agri. Res. Bull. 201, pp. 301–443.

GRAHAM, EDWARD H.

1944. Natural Principles of Land Use. xiii + 274 pp. New York: Oxford Univ. Press.

1947. The Land and Wildlife. xiii + 232 pp. New York: Oxford Univ. Press.

GRANGE, WALLACE BYRON

1949. The Way to Game Abundance, with an Explanation of Game Cycles. xviii + 365 pp. New York: Charles Scribner's Sons.

HORNADAY, WILLIAM T.

1913. Our Vanishing Wild Life: Its Extermination and Preservation. xvi + 411 pp. New York: Charles Scribner's Sons.

1914. Wildlife Conservation in Theory and Practice. vi + 240 pp. New Haven: Yale Univ. Press.

LEOPOLD, ALDO

1931. Report on a Game Survey of the North Central States. 299 pp. Madison, Wis.: Democrat Printing Co.

1933. Game Management. xxi + 481 pp. New York: Charles Scribner's Sons.

LONGHURST, WILLIAM M., A. STARKER LEOPOLD, and RAYMOND F. DASMANN

1952. A Survey of California Deer Herds, Their Ranges and Management Problems. Calif. Dept. Fish and Game, Game Bull. No. 6. 136 pp.

STODDARD, HERBERT L.

1931. The Bobwhite Quail: Its Habits, Preservation and Increase. xxix + 559 pp. New York: Charles Scribner's Sons.

TRIPPENSEE, REUBEN EDWIN

1948. Wildlife Management: Upland Game and General Principles. x + 479 pp. New York: McGraw-Hill Book Co., Inc.

WING, LEONARD W.

1951. Practice of Wildlife Conservation. viii + 412 pp. New York: John Wiley and Sons, Inc.